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ANATOMY OF *PHASEOLUS VULGARIS* ROOT—TIPS AS INFLUENCED BY GIBBERELLINS

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One of the most interesting groups of agricultural chemicals developed in recent years has been the gibberellins. A table compiled by Wittwer & Bukovac (1958) showed the effects of gibberellins on various economic plants as well as several physiological responses elicited by them.

As gibberellins have become more readily available, the number of studies has increased proportionally. Responses of plant roots to gibberellins have not been clearly defined as most studies have been based primarily on plants grown in nutrient culture (Stowe & Yamaki, 1957). In this brief communication, the effect of gibberellin on the roots of *Phaseolus vulgaris*, the sites of its greatest activity and the various anatomical changes induced by it in the roots are presented.

Material and Methods

Seeds of *Phaseolus vulgaris* 'Blue Lake' were sown on February 10, 25, April 1 and October 3, 1958 in 6 inch-clay-pots containing terralite. After the first leaves had developed, extra seedlings were rogued and the remainder paired. One plant of each pair was treated and the other served as a comparison. Plants were treated in a random block pattern.

Aqueous solutions containing Tween-Twenty[1] and Gibrel[2] were used for treatment. Plants were treated with 10 micrograms and 20 micrograms of gibberellin applied dropwise to the apices with a calibrated needle. Linear measurements of root extension were recorded 72 hours after treatment.

Severed root tips were killed and fixed in formalin-aceto-alcohol (FAA), dehydrated in the tertiary-butyl alcohol series, embedded in histowax, sectioned longitudinally at 10 microns, and stained with safranin—fast green. Average cell length was determined near the apical cell of permanent medial sections.

Additional plants were treated on March 24, April 18 and October 21 by saturating the media with 0, 20, 100 and 500 micrograms of an aqueous solution of gibberellins. After 72 hours, linear measurements of the shoot and root and the number of lateral roots were recorded. Shoot and root tips were killed and fixed in Randolph's modified Navashin solution, embedded, sectioned, and stained as previously described for microscopic examination. Specimens 8 mm in length were collected from the root tip, and at points 30 and 60 mm from the tip. Linear measurements were made of the cortical cells, 2, 30 and 60 mm from the apical cell and of epidermal cells 2 mm from the apical cell. Linear measurements of the roots were subjected to "Students t-test". An analysis of variance was performed on the cortical and epidermal cell length with respect to the various treatments. Significance was based on the multiple F test method of analysis (Duncan, 1955).

Observations and Results

Treated bean plants produced elongated stems and petioles with somewhat etiolated leaves. Leaves of treated plants

1. A wetting agent manufactured by the Atlas Powder Company, Wilmington, Delaware.
2. Potassium salt of gibberellic acid manufactured by Merck & Co. Inc., Rahway, New Jersey.

were more expanded than untreated plants. Roots of treated and non-treated plants on macroscopic inspection showed no apparent variation in diameters, fibrousness, color or number of lateral roots. Treated roots harvested 72 and 96 hours after treatment were similar to those from untreated roots. Only slight differences were observed in the length of cortical cells at the apex or 60 mm basipetal to it (Table 1) while cortical cells increased in length 30 mm from the apex after gibberellin treatment. Differences between untreated plants and those treated with 500 micrograms were not significant. Minor differences were observed between treatments of 100 and 500 micrograms, and between 20 and 100 micrograms. However, cortical cells from plants which received 20 to 100 micrograms of gibberellin were significantly longer than those of untreated plants. Plants treated with 20 micrograms of gibberellin showed the greater response.

Epidermal cells 2 mm basipetal to the apical cell did not respond to gibberellin treatment. Transverse sections of root segments 60 mm from the apical cell showed a delayed rate of lignification when compared with untreated root sections (Figs. 1, 2). Higher concentrations of gibberellin appeared to inhibit lignification and to increase the size of intercellular spaces.

Studies of root tips harvested 72 hours after treatment showed that the majority of cell divisions were anticlinal. No significant differences in the number of anticlinal divisions were recorded for treated and untreated plants. One periclinal division occurred in an untreated plant. An average of six sections showed four divisions in the central cylinder, and ten in the cortex of untreated plants; three divisions in the central cylinder and eight in the cortex of those treated with 500 micrograms of gibberellins.

TABLE 1

[*Influence of various concentrations of Gibberellins on the length of cortical cells in the root of Phaseolus vulgaris 'Blue Lake' at various distances from the apical cell (average of 14 cells). Gibberellins were applied to apices and plants were harvested 72 hours later.*]

Treatment (Micrograms per Plant)	Distance from Apical Cell (Length in microns)		
	2 mm	30 mm	60 mm
0	45	149	174
20	46	187*	184
100	44	174*	179
500	46	153	175
	N.S.	significant see below	N.S.

Micrograms			
0	500	100	20

A common line indicates no significance at 5 per cent.

*Significantly different from control at 5 per cent.

Discussion

Gibberellin treatment failed to increase the number or vigour of the roots of *Phaseolus vulgaris* 'Blue Lake'. Injuries that could be attributed to treatment were not observed.

Differences in root elongation at any concentration and by any method of application to shoot tip or the medium were not found. These results were similar to those of Lippert *et al.* (1958) who showed that gibberellins were freely translocated.

It was found that roots from untreated plants grow about 64 mm in 24 hours. Similar elongation did not occur during a comparable 24-hour period (72 to 96 hours after treatment) indicating an inhibition following treatment with 20 micrograms per milliliter of aqueous gibberellin solution. These results are confirmed by those of Brian & Grove (1957), who reported that in some instances gibberellins inhibited root growth. Apparently if inhibition is present, it extends for a longer time than the stimulatory effect.

The length of cortical cells was determined at the 2, 30 and 60 mm levels. Cortical cells were measured because they were more uniform than those of the various tissues of the central cylinder. Epidermal cells were measured only at the 2 mm level because those at the 30 and

FIGS. 1, 2 — Photomicrographs of longitudinal sections of *Phaseolus vulgaris* 'Blue Lake' roots 30 mm from the apical cell 72 hours after treatment. Fig. 1. Untreated; Fig. 2. Treated with 20 micrograms gibberellin, note elongated cortical cells on the left. × 187.

60 mm levels tended to slough. Only slight differences were observed in the epidermal cell length at any concentration. Cortical cells at the 2 mm level showed no difference at any concentration of gibberellin, but at the 30 mm level some response was found. Although the cortical cells at the 30 mm level elongated more rapidly in treated than untreated plants, the ultimate length of the cortical cell was not affected (Table 1), suggesting that gibberellins influenced rate of growth and not cell length in the time between treatment and harvest. Morgan & Mees (1956) reported similar results from a study of grass shoots where the total length was apparently not affected by gibberellin application. Lower concentrations induced a greater response than higher concentrations of gibberellins.

Reduction in lignification and increase in size of intercellular spaces was accompanied by an increase in cellular length.

Summary

Phaseolus vulgaris 'Blue Lake' plants grown under green house conditions were treated with 0, 10, 20, 100 and 500 micrograms of gibberellin. Treatment was made to determine the effect of gibberellin on the root and the site of its greatest activity.

Gibberellin was applied in different concentrations and with different methods. Linear measurements were recorded and permanent slides prepared from longitudinal sections of the root apices. Neither concentration nor method of application affected the total length of the root. Cortical cells of the root 30 mm from the apex appeared to elongate more rapidly in treated plants without affecting the ultimate cell length. Maximum effects were obtained with 20 and 100 microgram applications, 20 being more effective.

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THE MORPHOLOGY OF THE GRASS EMBRYO

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The grass embryo has been an object of study since 1687 (Malpighi) and of controversy for nearly 150 years. A list of publications expressing the diverse opinions includes about 80 references (Table 1). The various parts of the mature embryo have been judged to be many things, as indicated also in Table 1, and there is still wide diversity of opinion concerning these structures. There are numerous and diverse opinions for each of the structures involved.

Among embryos of the various taxonomic subgroups of the grass family there are some morphological variations (Reeder, 1957, for most recent treatment), but Figs. 1 and 2 will suffice to illustrate the controversial structures. The epiblast is uniformly present in the Chloridoideae and in most Festucoideae; it is absent in the Eupanicoideae. The scutellum, coleoptile, coleorhiza, endogenous root and plumule are present in all grass embryos. The mesocotyl is present, at least during early seedling development, in almost all grasses although it is not developed in barley and only slightly in wheat. Mesocotyl elongation (during germination in absence of light) is accomplished by an intercalary meristem. If this transverse meristem is initiated above the procambial strand to the scutellum, as in the Panicoideae, wheat, etc., this strand is not altered during germination but runs directly to the scutellum in the young seedling (Fig. 3). If the meristem is initiated across the loop of this strand, the ascending and descending portions of the strand are greatly elongated vertically, as in *Avena* (Fig. 4), with the xylem external to the phloem in the descending portion (Arber, 1934; Yakovlev, 1950).

There is no disagreement as to the morphology of the mature grass embryo. The problem arises from the interpretations of what these structures represent. A brief summary of proposals for the embryonic structures follows (*see* also Table 1).

The *scutellum* is generally considered to be either the entire cotyledon or part of the cotyledon. Nevertheless, it has also been considered to be a transition between the endosperm and the cotyledon (Gaertner, 1788), a lateral protruberance of the radicle (Richard, 1811; Cassini, 1820; de Jussieu, 1839; Hofmeister, 1861; Sachs, 1862; Gris, 1864; Lermer & Holzner, 1886), a thallus outgrowth of the axis (Sandéen, 1869), an aborted terminal bud (Reisseck, 1843), the true embryonic axis (Jacques-Felix, 1957), or equivalent to a floret peduncle or leaf sheath (Raspail, 1824). While most authors consider it the single cotyledon, others consider it one of two cotyledons, the first of two (Roth, 1955) or the second of two (Bugnon, 1921; McCall, 1934). When considered to be part of the cotyledon, it has been called a blade, stipule, bract or sucker.

The *coleoptile* has been considered to be the cotyledon, part of the cotyledon, such as the sheath, (Bernhardi, 1832; Sargant & Arber, 1915; Toole, 1924; Goebel, 1905) or ligule (Schleiden, 1837; van Tieghem, 1872; Celakovsky, 1897; Kennedy, 1899; Cannon, 1900; Worsdell, 1916; Arber, 1934), a palea or prophyll (Raspail, 1824), an axillary bud (Reisseck, 1843), a leaf sheath (Demoor, 1853), a trichomatic projection (Hanstein, 1870), a leaf (1st, 2nd, or 3rd leaf), two fused leaves (Godron, 1897), two cotyledons grown together (Lestiboudois, 1848), or the 3rd part of the single cotyledon (McLean & Ivimey-Cook, 1956).

The *mesocotyl* has been called an internode, a node, fusion of hypocotyl and part

TABLE 1 — CONCEPTS OF VARIOUS AUTHORS, HISTORICALLY ARRANGED

NAME	SCUTELLUM	COLEOPTILE	EPIBLAST	MESOCOTYL
Malpighi 1687[1,2]	Cotyledon	—	—	—
Gaertner 1788[1,2]	Transitional between endosperm & cotyledon	—	—	—
Poiteau 1809[1,2]	1st cotyledon	—	2nd cotyledon, rudiment	—
Richard 1811[1,2]	Lateral protuberance of radicle	—	Root sheath (coleorhiza ?) continuation	—
Mirbel 1809, 1810[1,2]	1st cotyledon 1809	Cotyledon part 1801	2nd reduced cotyledon, 1809	—
Treviranus 1815	Cotyledon	—	—	—
Turpin 1819[1]	1st cotyledon	—	2nd cotyledon	—
Cassini 1820[1]	Lateral protuberance of radicle	Cotyledon	—	—
Raspail 1824[1,2]	Floret peduncle, also leaf sheath	Palea and also prophyll	—	—
C. A. Agardh 1826[1]	Cotyledon cover	—	—	—
de Candolle, A.P. 1827[1]	—	—	2nd cotyledon	—
Bernhardi 1832[1]	Cotyledon	Sheath of cotyledon	—	—
Bischoff 1830, 1834[1,2]	1st cotyledon	—	2nd cotyledon	—
M. J. Schleiden 1837, 1839[1,2]	Blade of cotyledon	Ligule of cotyledon	Cotyledonary outgrowth	—
Mirbel & Spach 1839	Cotyledon	3rd leaf	2nd leaf	—
A. de Jussieu 1839[1,2]	Lateral axis appendage	Cotyledon	—	—
Regel 1843[1]	Stipule or bract	Cotyledon	—	—
Reisseck 1843[1]	Aborted terminal bud	Sheath of axillary bud	Part of cotyledon	—
Lestiboudois 1848[1]	Unimportant, no fibrovascular bundles	Cotyledon (2 leaves grown together)	—	—
Hofmeister 1849[2]	Part of cotyledon	Part of cotyledon	—	—
Demoor 1853[1,2]	Cotyledon	Primordial leaf sheath	—	—
Schacht 1862[1]	Cotyledon, part	2nd leaf	Part of cotyledon	—
Hofmeister 1861[1,2]	Lateral outgrowth of axis, not a leaf	Outgrowth of mesocotyl	—	—
de Saint-Pierre cited by Gris	Part cotyledon, part axis	—	—	—
Gris 1864[1,2]	Lateral outgrowth of axis	Cotyledon	—	*" Collet "*
Le Maout et Decaisne 1868[1]	Cotyledon	1st leaf	Insignificant	—
Sandéen 1868[1,2]	Thalloid growth	—	—	—
Sachs 1862 & 1882[1,2]	Axial outgrowth	Outgrowth of mesocotyl	—	—
Hanstein 1870[1,2]	Cotyledon	Trichomatic projection	Trichomatic projection	Node
van Tieghem 1872[1,2]	Blade of cotyledon	Ligule of cotyledon	—	Node
Hagelmaier 1874[1,2]	Part of cotyledon	Part of cotyledon	Rudimentary cotyledon	—
Wilson 1879[1]	Cotyledon	Probably leaf sheath	—	—
de Bary 1884	—	—	—	Internode
Warming 1895[1]	Cotyledon	Leaf	2nd cotyledon	—
Klebs 1881/85[1,2]	Part of cotyledon	Part of cotyledon	—	—
Hackel 1887[1]	Cotyledon	1st leaf	2nd cotyledon	—

TABLE 1 — CONCEPTS OF VARIOUS AUTHORS, HISTORICALLY ARRANGED—*contd.*

NAME	SCUTELLUM	COLEOPTILE	EPIBLAST	MESOCOTYL
Holzner 1890[1,2]	Expansion of hypocotyl	—	—	—
Norner 1881[2]	—	Cotyledonary sheath	—	—
Douliot 1891[2]	Part of cotyledon	Part of cotyledon	—	Node
Bruns 1892[1,2]	One cotyledon	1st leaf sheath	2nd cotyledon	Internode
Schlickum 1896[1,2]	Part of cotyledon	Part of cotyledon	Outgrowth of coleorhiza	—
Celacovsky 1897[1,2]	Blade of 1st cotyledon = blade of leaf	Ligule of cotyledon	Appendage of scutellum, Second cotyledon	Node
Godron 1897[1]	—	Two fused leaves	—	—
van Tieghem 1897 & 1898[1,2]	1st cotyledon	1st leaf	2nd cotyledon	Internode in some, Node in others
Kennedy 1899	Cotyledon, blade	Cotyledon, ligule	2nd cotyledon	Node
Cannon 1900[2]	Cotyledon	Ligule of cotyledon	Perhaps 2nd cotyledon	—
Goebel 1905[2]	Part of cotyledon	Sheath of cotyledon	Outgrowth of coleorhiza	Node
Coulter 1915[2]	Cotyledon	Leaf	2nd cotyledon	Internode
Sargant & Arber 1915[2]	Sucker of cotyledon	Sheath of cotyledon	Outgrowth of cotyledon or axis	Fusion of hypocotyl and part of cotyledon
Worsdell 1916[2]	Blade of cotyledon	Ligule of cotyledon	Auricle of cotyledon	Node
Bugnon 1921[2]	2nd cotyledon	Part of 2nd cotyledon	1st cotyledon	Node
Nishimura 1922	Part of cotyledon	Part of cotyledon	—	—
Weatherwax 1920[2]	Lateral cotyledon	Leaf	—	Internode
Toole 1924[2]	Cotyledonary sucker	Sheath of cotyledon	Ourgrowth of cotyledon	—
Souèges 1924[2]	Part of cotyledon	Part of cotyledon	—	—
Howarth 1927[2]	Part of cotyledon	Part of cotyledon	—	—
Percival 1927[2]	Cotyledon	3rd leaf	2nd leaf	" Rhizome "
Avery 1930[2]	Cotyledon	Leaf	Insignificant growth	Internode
Boyd 1931[2]	Cotyledon	Leaf	" Ligule " of cotyledon	Internode
Arber 1934	Part of cotyledon	Ligule of cotyledon	Mere epidermal outgrowth	Node
McCall 1934[2]	2nd leaf (cotyledon)	3rd leaf (prophyll)	1st leaf (cotyledon)	2nd internode
Reznik 1934[2]	Part of cotyledon	Part of cotyledon	—	Node
Randolph 1936[2]	Cotyledon	1st leaf	—	—
Boyd & Avery 1936[2]	Cotyledon	Leaf	Ligule of cotyledon	Internode
Yakovlev 1937	—	Leaf	—	—
Buchet 1938[2]	Lateral expansion of cotyledon	Principle part of cotyledon	Not more than a rudiment	—
Yung 1938	Cotyledon	2nd leaf	Probably not a cotyledon	—
Campbell 1940[2]	Part of cotyledon	Part of cotyledon	—	—
Merry 1941[2]	Same origin but not homologous with foliage leaves; peculiar to embryo. Cotyledon		—	Partially axis plus some scutellum or coleoptile
Mullendore 1948	Cotyledon	—	Outgrowth of scutellum	Internode
Kiesselbach 1949	Cotyledon = 1st leaf	2nd leaf	—	—

TABLE 1 — CONCEPTS OF VARIOUS AUTHORS, HISTORICALLY ARRANGED—*contd.*

NAME	SCUTELLUM	COLEOPTILE	EPIBLAST	MESOCOTYL
Mimeur 1950[2]	Cotyledon	2nd leaf	—	—
Troll 1954[2]	Part of cotyledon	Part of cotyledon	—	Node
Strasburger 1954[2]	Blade of leaf	Ligule of leaf	Scutellar appendage	Part of cotyledon
Firbas 1954[2]	—	Part of cotyledonary sheath	—	—
Sass 1955	Cotyledon	Outgrowth of scutellum	—	Internode
Roth 1955	1st cotyledon	1st leaf	2nd cotyledon	—
McLean & Ivimey-Cook 1956	1st part of cotyledon	3rd part of cotyledon	Possibly a ligule	2nd (middle) part of cotyledon
Reeder 1956	—	Leaf	—	—
Jacques-Felix 1957	Embryonic axis	Prophyll	Subtending leaf	Internode
Tucker 1957	—	—	—	Internode
Brown 1959	Part of cotyledon	Part of cotyledon	Outgrowth of coleorhiza	—

1. For reference *see* Kennedy, 1899, or Brunus, 1892.
2. For reference *see* Roth, 1955.

of the cotyledon (Sargent & Arber, 1915), " rhizome " (Percival, 1927) or the middle of three parts of the cotyledon (McLean & Ivimey-Cook, 1956).

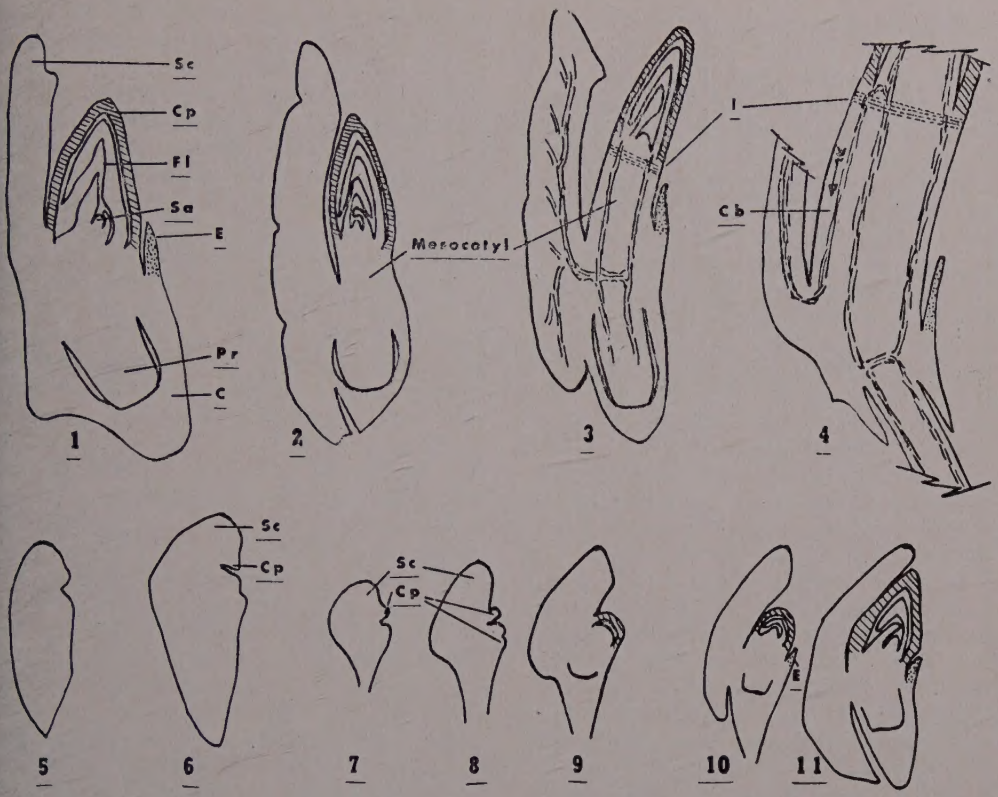
The *epiblast*, it has been claimed, is a 2nd cotyledon, the 1st cotyledon (Bugnon, 1921; McCall, 1934), part of the single cotyledon such as an auricle (Worsdell, 1916) or ligule (Boyd, 1931; Boyd & Avery, 1936; McLean & Ivimey-Cook, 1956), a trichomatic projection (Hanstein, 1870), outgrowth of cotyledon or axis (Sargant & Arber, 1915), a leaf (Percival, 1927), a subtending leaf (Jacques-Felix, 1957), or a mere outgrowth of the coleorhiza (Richard, 1811; Schlickum, 1896; Avery, 1930; Arber, 1934; Goebel, 1905; Brown, 1959).

Finally, Merry (1941) has proposed that the scutellum and coleoptile are structures peculiar to the embryo, that there is no conclusive evidence that they are modified foliage leaves.

It is evident that even among recent studies there is still wide disagreement concerning the homologies of these structures.

Most opinions about the embryonic structures have been based upon studies of mature embryos only; but studies of the time and place of development of these parts during embryogeny have been revealing and valuable. As in all angiosperms, a more or less spherical proembryo develops from the zygote. The first evidence of structural differentiation is a notch in one side (Figs. 5, 6, 7). From just above the notch, an outgrowth of the original proembryo develops outward at the same time so that the remainder of the adjacent upper part of the proembryo begins rapid development into the eventual scutellum. The outgrowth just above the notch is the beginning of coleoptilar development. The tissue just below the notch eventually develops into the shoot apex around which the base of the coleoptile extends until it completely surrounds the shoot apex (Figs. 8, 9) and often completely covers it like a hood.

At about this stage of development the primary root differentiates endogenously; the remaining tissue external to the root is the coleorhiza. Subsequently, in many species, there is an outgrowth from the coleorhiza, on the side opposite to the scutellum, that becomes the epiblast (Fig. 10). Later, as the shoot apex produces one or more leaf primordia there is, in many species, the development of a short mesocotyl between the attachment of the scutellum and the base of the



FIGS. 1-11 — Longitudinal median sections of grass embryos of various ages (*Sc*, scutellum; *Cp*, coleoptile; *Fl*, foliage leaf; *Sa*, shoot apex; *E*, epiblast; *Cr*, coleorhiza; *Pr*, primary root; *I*, intercallary meristem; *Cb*, cortical bundle, the descending part of the scutellar bundle during germination in *Avena* and many other grasses). Fig. 1. Mature ungerminated embryo of *Triticum aestivum*. Fig. 2. Same of *Zea mays*. Fig. 3. A germinated embryo of *Triticum aestivum*. The mesocotyl has elongated and a meristematic zone formed. Scutellar bundle unchanged. Fig. 4. Germinated embryo of *Avena sativa*. Mesocotyl has elongated. The meristematic zone has lengthened both the ascending and descending portions of the scutellar bundle. Figs. 5-7. Early embryonic differentiation in *Hordeum sativum*, *Brachypodium*, and *Tridens pilosus* respectively. Figs. 8-11. Stages embryo development of *Tridens pilosus*. Epiblast initiation is in late stage of development in Fig. 10. Figs. 1, 3, and 4 after Avery, 1930. Fig. 5 after Merry, 1941. Fig. 6 after Hanstein, 1870. Figs. 7-11 after Brown, 1959.

coleoptile (Fig. 2). Growth and development stop at about this stage, the scutellum in the meantime having developed into a large structure in contact with the abundant endosperm. Procambial strands to the scutellum, coleoptile, first leaf, and root have in the meantime been laid down.

It is justifiable to criticize the conclusions of a large number of authors, as Johansen (1950) implied, since they were based upon examination of mature embryos only, or mature embryos and young seedlings. It is my opinion also that knowledge of the place and time of origin of some of these embryonic structures is essential to proper understanding. Furthermore, comparisons of the grass embryo with embryos of other Monocotyledons, especially of the Cyperaceae, is very important.

Interpretation is also influenced by preconceived ideas. Of the 80 published interpretations listed in Table 1, all authors except Sachs (1882), Merry (1941), and Brown (1959) have assumed that cotyledons are leaves or are homologous

with foliage leaves, whatever such a statement means. The basis for this concept is the "Doctrine of Metamorphosis" of Goethe (1790), who, however, deliberately omitted consideration of "the single cotyledons of indefinite form belonging to those plants which germinate with one leaf," (part I, paragraph 17, after Arber, 1946, p. 94).

Numerous others have assumed that Monocotyledons and Dicotyledons have had a common origin, the Monocotyledons having more or less lost one cotyledon (Sargant, 1902). Interpretations have been influenced remarkably by these correct or incorrect concepts. It is impossible that all proposals can be correct because many are restrictive and limiting, nor can a synthesis including all be reached, nor can truth be reached by a statistical average compromise of opinions.

It seems to me that the problem exists mainly because of probably incorrect preconceived concepts, the loose use of such terms as leaf, foliage leaf, node, internode, and cotyledon, and because too few opinions have been based upon embryo development and comparison with other monocotyledonous embryos. I base my attitudes toward the parts of the mature embryo upon origin and sequence in embryogenesis. The time seems to be appropriate now for a reconsideration of what the structures of the grass embryo are most likely to be.

The first consideration is an examination of the concepts of the leaf and the cotyledon and an attempt to define them. During early development of the young vascular plant sporophyte two requirements, among others, must be met. The young sporophyte must take in organic food from some outside source, such as the female gametophyte or endosperm. Among the vascular cryptogams a so-called foot is developed for this activity; among spermatophytes the cotyledon does it. Lyon (1902) considered cotyledons to be primarily haustorial organs and not arrested foliage leaves. A second necessity is the early establishment in the light of an adequately extensive photosynthetic tissue. Sufficient photosynthetic activity must be established before the reserve food of gametophyte or endosperm is exhausted. Among the vascular cryptogams the cotyledon does this. Among most spermatophytes also, the cotyledon or cotyledons reach the light early. However, if some other photosynthetic tissue can be established in the light soon enough, the cotyledons may be freed from that responsibility. Among seed plants, therefore, cotyledons have two basic functions, food intake and photosynthesis; but food intake may be completed before the seed is mature, or the cotyledon may not become a photosynthetic organ if other structures take over that responsibility or if the whole plant lacks chlorophyll as in *Cuscuta*. Additional or new structures may then be developed from the cotyledon, or part of it, which function in soil penetration, plumule protection, etc. A change of function is usually accompanied by a change of structure, or a uniquely new function may be associated with a novel structure.

Does the photosynthetic activity of a cotyledon make it a leaf? Is a phylloclade a leaf? Just what is a leaf and what is a cotyledon? In all vascular plants the cotyledon originates directly from part of the proembryo. Foliage leaves (phyllomes) always develop as lateral outgrowths from apical meristems of stems (Wardlaw, 1956). As to origin, then, cotyledons and foliage leaves are quite distinct, neither is homologous with the other. They may develop into structures that look and function alike just as phylloclades may look and function as foliage leaves but are not homologous with them (*see* Coulter & Chamberlain, 1903 for: Lyon, 1902; Balfour, 1901). The genes that determine the morphology of the foliage leaves may also determine a similar shape in cotyledons. Goebel (1905) considered cotyledons to be developmental forms of foliage leaves because of (1) analogy with cotyledons of Pteridophytes, (2) because they look like leaves, and (3) because there are all intermediate types between cotyledons and foliage leaves. De Candolle (1827) gave a similar but longer list of reasons for homology. Coulter & Chamberlain (1903) took an intermediate position stating that "The current opinion regards the cotyledon as a modified foliage leaf and this is

borne out in the majority of Dicotyledons by the assumption of the foliage function. The terminal cotyledon of Monocotyledons, however, seems to belong to a different category, and to hold no relation to a foliage leaf or to a foliar member of any description." Later (Coulter & Land, 1914) the cotyledons, whether one, two or more, were considered to be lateral structures with a common basis of origin, the number of cotyledons being a secondary feature.

Sachs (1882), on the other hand, stated that if the apical part of the monocotyledonous proembryo is really the cotyledon then it can not possibly be a foliar structure (phyllome), even if subsequently it assumes altogether the appearance of a foliage leaf. I believe Sachs has the stronger position. Admittedly, cotyledons may look like leaves, but they often do not, especially among Monocotyledons. A number of authors have made comparative studies of various monocot embryos with grass embryos. There are no known foliage leaves comparable to many of the unique cotyledons described, such as those of the coconut, the Commelinaceae, the Cyperaceae, and the Gramineae. Cotyledons, when freed of their basic photosynthetic activity have often specialized into structures as remarkably different from foliage leaves as some of them are equally remarkable in their resemblance to foliage leaves. It does not seem to me that mere resemblance is adequate for the establishment of homology between cotyledons and foliage leaves any more than between other somewhat similar biological pairs of structures (Arber, 1954).

If phyllomes and cotyledons are not homologous, the attempt of so many authors to homologize them in the grass embryo has led to much of the persistent confusion. If a cotyledon is not homologous with a foliage leaf, it is not necessary that it should have a sheath, blade, ligule, auricles, or other foliage leaf structure. The cotyledon, then, is peculiar to the embryo, as Merry (1941) has stated, and has been able to differentiate in peculiar ways and into unique structures that may have no counterparts among foliage leaf. Thus, in the grass embryo, the apical portion of the proembryo gives rise to two structures, the scutellum and the coleoptile, that may be conceived as two distinct parts of the cotyledon or more correctly, as two quite different structures that develop from the same portion of the proembryo. In either case they are in no sense homologous with foliage leaves. Efforts, such as those of Reeder (1953, 1956), to find a coleoptile with a median bundle and when one is found to accept that as proof that the coleoptile is a foliage leaf, or of Jacques-Felix (1957) to demonstrate that the epiblast is a subtending leaf, the coleoptile a prophyll, and the plumule an axillary bud with the scutellum the main embryonic axis, are not contributing to a clarification of the problem.

The mesocotyl is another structure that has been interpreted as homologous with shoot structures. It is usually considered to be a node or an internode. Yet it also originates directly from the proembryo, whereas nodes and internodes are derived from stem apices. The mesocotyl is neither a node nor an internode but a structure peculiar to the embryo. It originates from tissue that, in the proembryo, lay below the shoot apex, but in the mature embryo and young seedling the mesocotyl occupies a position between the attachment of the scutellum and the base of the coleoptile. Furthermore, it is unlike an internode since the intercalary meristem remains just below the coleoptile, above the tissue it produces, whereas the intercalary meristem of an internode remains below the tissue it produces. On the other hand, to describe as a node a structure that has an intercalary meristem and that can elongate remarkably is also impossible. A node is a transverse region of stem at which one or more leaves are attached. Of course, if the coleoptile and scutellum are not leaves nor homologous with leaves, then the mesocotyl cannot be a node nor an internode since those cauline structures are produced by apical meristems and subsequent differentiation.

The epiblast is formed late in embryogeny (Roth, 1955; Brown, 1959; Streetman & Wright, 1960) as an outgrowth of the coleorhiza after the scutellum, coleoptile, plumule, and root have begun differentiation. Unless one has a preconceived belief that Monocotyledons have been derived from Dicotyledons, a

completely unproved hypothesis, the student of grass embryonic development would hardly consider the epiblast to be a cotyledon. Its time and place of origin, its cellular structure, and function (the production of coleorhizal hairs early in germination) all indicate that it is no more than an upward extension of the coleorhiza (Brown, 1959, and others). Like the scutellum, coleoptile, and mesocotyl, it is an unusual structure peculiar to embryos of certain species of grasses. It is certainly not homologous with a leaf, a product of a stem apex, nor homologous with a cotyledon, a structure that arises directly from the proembryo at the very beginning of differentiation.

The recent suggestion by Pashkov (1951) that the coleorhiza is the true embryonal root, and that the differentiated endogenous root is of lateral or adventitious origin would seem fantastic if applied to the embryo of any plant other than a grass. It is not startling, however, as a suggestion for the grass embryo. There have been so many unusual suggestions for that structure that Pashkov's suggestion is quite in context and rapport.

If the structures of the grass embryo are considered to be the products of embryonic differentiation and not homologous with the products of shoot apex activity, there is no problem. But if they are considered to be homologous with leaf and stem structures, then a wide selection of possible interpretations is available. Almost all of the possibilities, however, seem to have been preempted during the past 150 years. However, a fertile imagination need not be discouraged, novel homologies are still possible (Jacques-Felix, 1957).

These grass embryo structures can be described as caenogenetic innovations of ontogeny that have evolved and have usefulness only during germination, according to the concept of Beer (1951) in his excellent discussion " Embryos and ancestors ". In it he stated (p. 41), " It is clear, then, that evolutionary novelties do arise in the early stages of development and may restrict their effects to those stages." Such novel structures are completely unrelated to structures of the mature plant; they have had their own distinct evolution. Some of such caenogenetic changes may give rise to new characters of basic systematic significance. Such a case of deviation during the very earliest stages of embryonic development was the substitution of one cotyledon for two (Takhtajan, 1945, according to de Beer, p. 49) just as among Dicotyledons there is probably a reduction from three or four, as found in the primitive dicotyledon *Degeneria vitiensis* (Swamy, 1949) and in a few cases to one (Lyon, 1901; Conrad, 1902; Metcalfe, 1936; etc., *see* Wardlaw, 1955, p. 262), thereby producing the monocotyledonous dicotyledons (Sargant, 1903; Coulter & Land, 1914) for some of which van Tieghem (1898) created a taxon equivalent to the Monocotyledons and Dicotyledons. Among the endospermless Orchidaceae the single cotyledon, if formed at all, is rudimentary (Goebel, 1905).

De Beer also points out the weakness of relying upon particular gene effects in phylogenetic relationships. Such an argument suggests that the same pleiotropic genes that determine the anatomy and morphology of the foliage leaf could also affect photosynthetic cotyledons and result in a certain resemblance inspite of their being not homologous.

The study of embryonic differentiation strongly suggests that these embryonic structures are peculiar to the embryo and not homologous with foliage leaves, nodes, nor internodes. Belief in homology, on the other hand, is based on the unproved hypothesis, that, because many cotyledons do resemble foliage leaves somewhat, cotyledons and foliage leaves are homologous. Similarity can best be regarded as analogy. Because leaves and most cotyledons are photosynthetic structures it is inevitable that they must be somewhat similar morphologically. However, when true foliage leaves develop quickly during germination and relieve the cotyledon of one of its basic functions, photosynthesis, the cotyledons of many Monocotyledons have differentiated in part, or new structures have developed directly from the proembryo for additional new functions. Two of these functions in grasses are the penetration of soil and protection of the plumule by the coleoptile and elongation by the mesocotyl to raise the plumule and coleoptile to the surface

of the soil. Digestion of the endosperm, absorption of the organic foods produced, and transport to the root and plumule, basic functions of the cotyledons of seed plants, are the functions of the scutellum, the cotyledon.

Summary

I regard the scutellum as the cotyledon that retains one of the cotyledonary functions, that of absorption of digested endosperm during germination. The coleoptile and mesocotyl are caenogenetic innovations developed during ontogeny directly from the proembryo, but they are not cotyledonary. The mesocotyl is analogous to the hypocotyl of the Dicotyledons. The epiblast is a lateral upward outgrowth of the coleorhiza, no more. The coleorhiza is the tissue that remains external to the radicle when that structure forms endogenously.

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MORPHOLOGICAL AND EMBRYOLOGICAL STUDIES IN THE FAMILY LORANTHACEAE—VI. *PERAXILLA TETRAPETALA* (LINN. F.) VAN TIEGH.

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The genus *Peraxilla* embraces six species distributed mostly in Australia and New Zealand. The species included under *Perella* by Van Tieghem[1] (1895) were transferred by Danser (1933) to the earlier genus *Peraxilla* since the differential characters described by Van Tieghem were not distinguishable in the Kew specimens. The slight difference in the presence or absence of a short pedicel was regarded by Danser as insufficient for generic distinction.

So far there has been no embryological work on *Peraxilla*. The following account deals with the morphology and embryology of *P. tetrapetala* (Linn. f.) Van Tiegh.

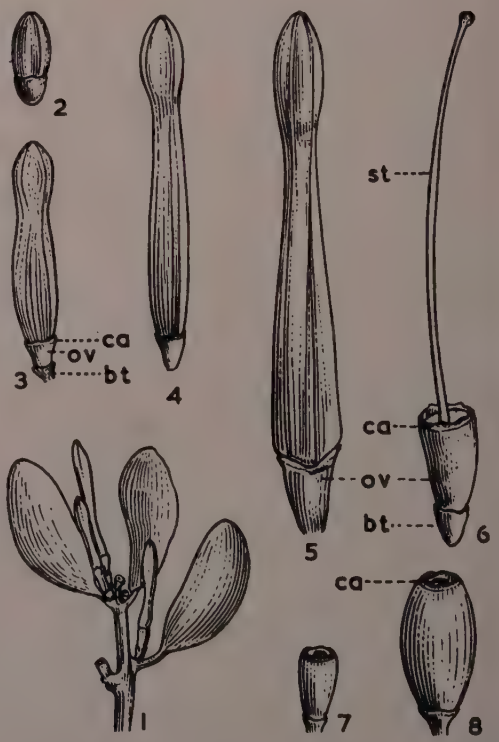
Material and Methods

Buds, flowers and fruits of *P. tetrapetala* preserved in formalin-acetic-alcohol were obtained from New Zealand through the courtesy of Professor G. Brownlie to whom I am very grateful.

The usual methods of dehydration and embedding were followed. Sections were cut 5 to 20 microns thick and stained with safranin-fast green. Developmental stages of female gametophyte, endosperm and embryo were also studied from dissections. For this the material was pretreated with five per cent potassium hydroxide and cleared in lactophenol.

Observations

Floral Morphology — The flowers are shortly pedicelled, tetramerous and arranged in a raceme (Fig. 1). A small persistent bract develops at the base of the ovary (Figs. 3, 6). The calyculus forms a short tube around the corolla[2] (Figs. 2-4) and persists in the fruit (Figs.



Figs. 1-8 — All figures diagrammatic. (*bt*, bract; *ca*, calyculus; *ov*, ovary; *st*, style). Fig. 1. Inflorescence. × ¾. Figs. 2-5. Developmental stages of buds. × 2. Fig. 6. Ovary with style. × 2. Figs. 7, 8. Young and mature fruits. × 2.

1. Quoted in Danser (1933).

2. Since the calyculus has been shown to represent calyx (*see* Narayana, 1958b; Garg, 1958), the perianth has been designated here as corolla.

7, 8). The corolla is polypetalous and due to the interlocking of the adjacent epidermal cells the petals remain attached to one another in the young bud. In the mature bud, the corolla tube is hastately dilated at the base, gradually narrows above and again becomes broad towards the tip (Fig. 5). There are four epipetalous stamens, adnate with the petals for one-third the length of their filaments. The anthers are basifixed and introrse and dehisce in the bud condition. The gynoecium is tetracarpellary and the style ends in a capitate stigma (Fig. 6). At the base of the style there are four small protuberances which probably function as nectaries. The fruit is an obovoid pseudoberry (Figs. 7, 8).

ORGANOGENY — The floral primordium appears as a small protuberance in the axil of a bract and the different organs arise in acropetal succession. The calyculus differentiates as a small rim. In earlier stages the ovary is at the same level as the petals (Fig. 40) but subsequently the gynoecium becomes inferior in position (Fig. 41). At first the stylar canal is wide and continuous with the ovarian cavity but as the bud matures it becomes narrow in its basal portion. Concomitantly a conical projection called the mamelon develops at the base of the ovarian cavity (Figs. 41, 42).

VASCULAR ANATOMY OF FLOWER — The stele of the pedicel supplies two vascular traces to the bract and just below the level of the ovary it comprises four vascular bundles (Figs. 9, 10). At a higher level these bundles divide (Figs. 11, 12) and become arranged in a ring consisting of four groups of five bundles each alternating with a single bundle (Figs. 13, 14). These last four bundles directly enter the style and bifurcate in the stigma. Each group of the five bundles reorganises in such a way that two of the bundles come to lie on the inner side (Figs. 15, 16). Both these groups of bundles traverse the adnate portion of the petals and stamens (Fig. 16). Ultimately the outer three bundles enter each petal and the inner two pass into the adjacent stamen (Figs. 17, 18). In the upper part of the petals the two lateral bundles divide so that there are five strands. The two traces of each stamen (Fig. 17) fuse in the region of the anthers (Fig. 18). There is no vascular supply to the calyculus (Fig. 16).

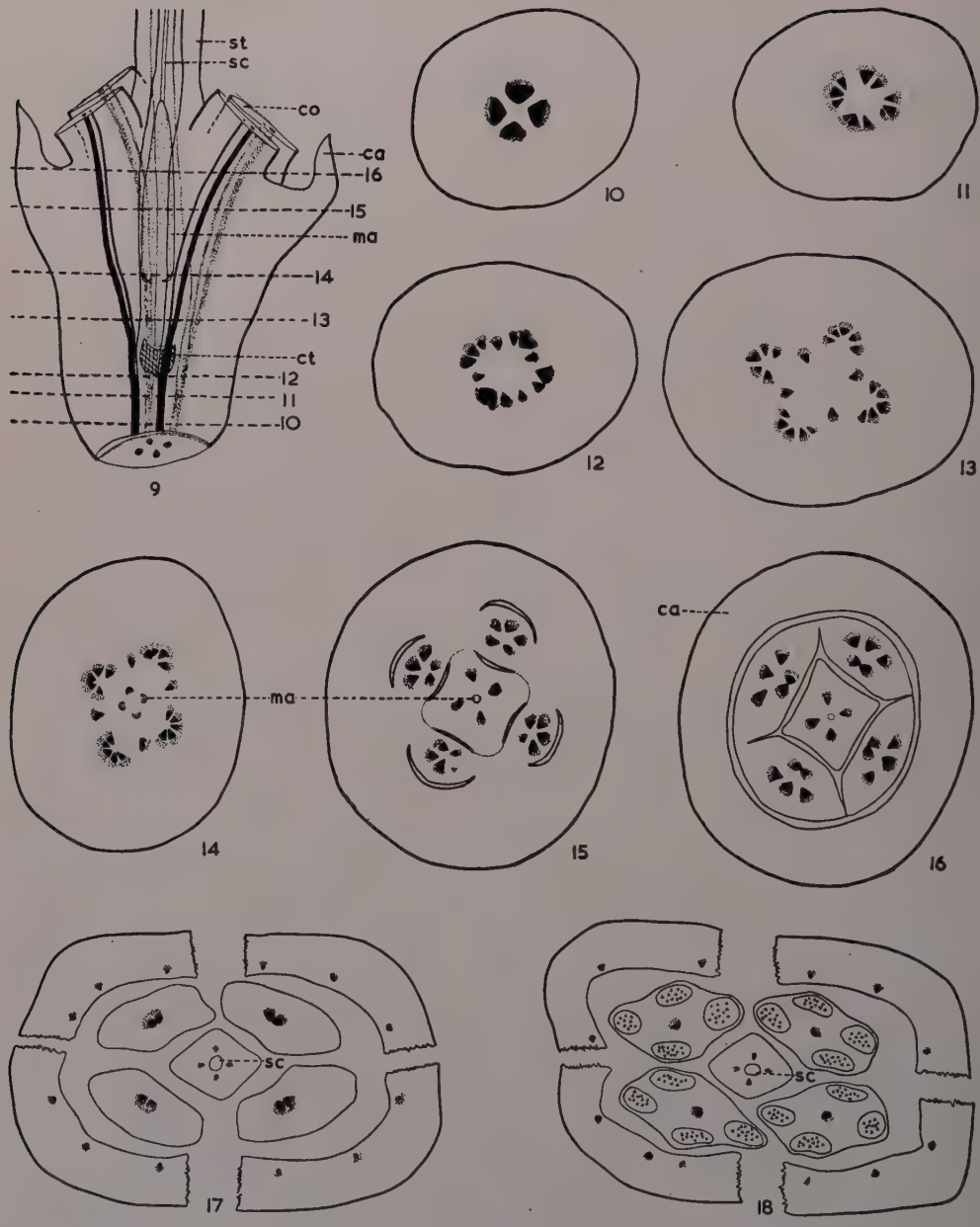
MICROSPOROGENESIS AND MALE GAMETOPHYTE — The anther consists of four microsporangia (Figs. 18, 19) which dehisce individually (Fig. 27) by a longitudinal slit.

A hypodermal archesporium differentiates in each lobe of the young anther. Its outermost layer divides periclinally cutting off the primary parietal layer. The latter undergoes periclinal divisions and of the two layers thus produced, the outer forms the endothecium while the inner divides again giving rise to the middle layer and the tapetum. Sometimes the middle layer may also divide so that the anther wall comprises the epidermis, endothecium, one or two middle layers and the tapetum (Fig. 20).

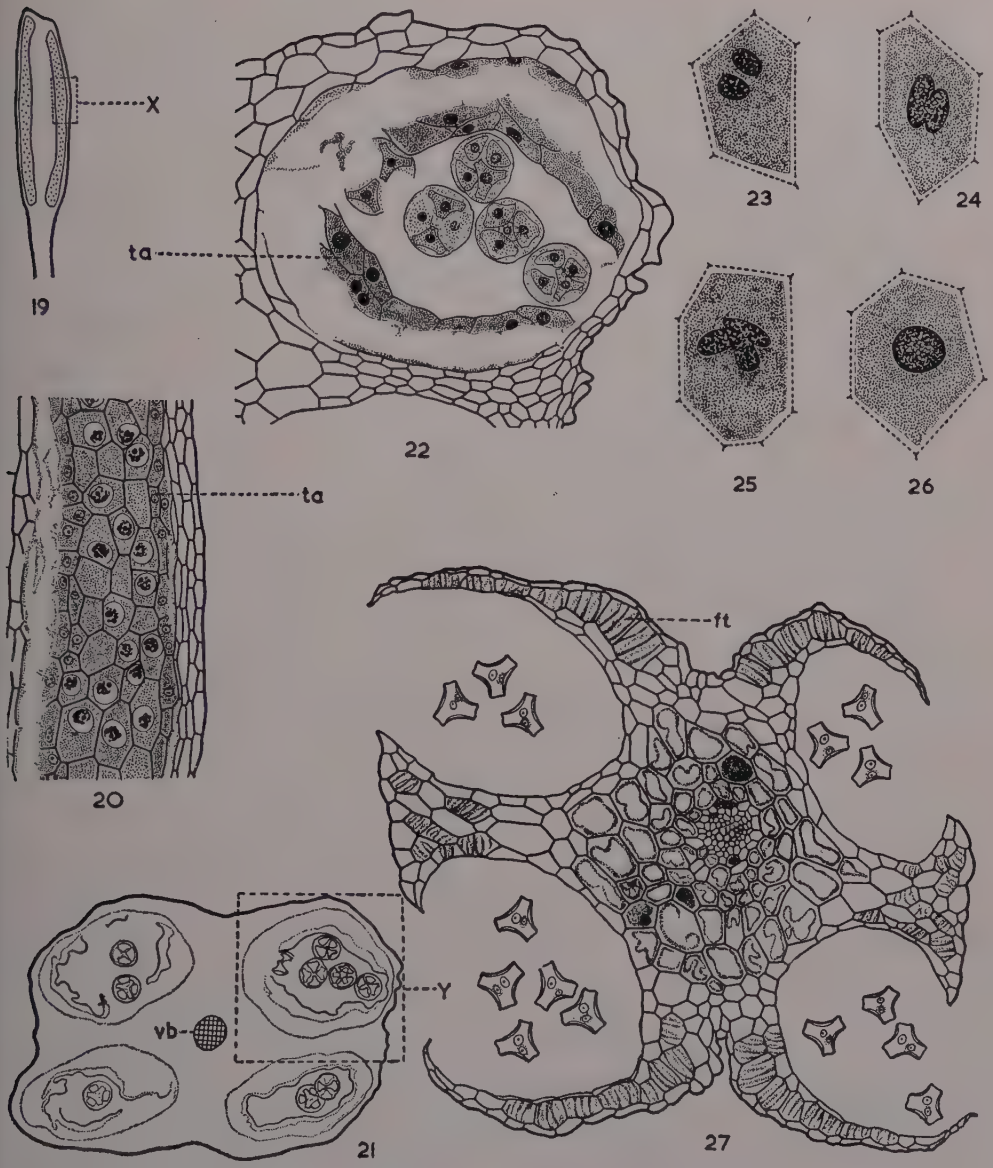
The epidermal cells become flattened but remain intact even in a dehisced anther (Fig. 27). The cells of the endothecium elongate radially and develop fibrous thickenings (Fig. 27). The middle layer is ephemeral and collapses even before the reduction divisions are over.

The tapetum is glandular and most of its cells show two (sometimes three) nuclei (Fig. 23) even before the microspore mother cells have entered meiosis. During the reduction divisions the tapetal nuclei often fuse resulting in a polyploid condition (Figs. 24-26). At places the tapetal cells may divide periclinally (Figs. 20, 22). The tapetum shows signs of degeneration at the 2-celled stage of the pollen and is almost wholly absorbed during its maturation (Fig. 27).

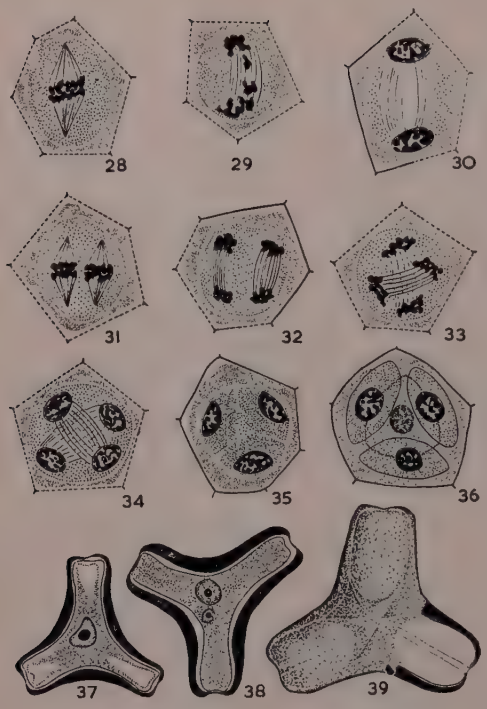
In each anther lobe the sporogenous cells divide to form a large number of polygonal microspore mother cells which are richly cytoplasmic (Fig. 20). A mucilaginous substance is secreted between the receded protoplast and the original wall of the microspore mother cells. The reduction divisions are simultaneous (Figs. 28-34) and cytokinesis occurs by furrowing (Fig. 35) followed by centripetal wedges of the mucilaginous wall which meet in the centre (Fig. 36). Both decussate and tetrahedral types of tetrads are formed (Figs. 22, 36). In a tetrad



FIGS. 9-18 — (*ca*, calyculus; *co*, corolla; *ct*, collenchymatous tube; *ma*, mamelon; *sc*, stylar canal; *st*, style). Fig. 9. Ovary from a cleared whole mount showing disposition of vascular traces (diagrammatic). × 18. Figs. 10-18. Serial transections of a bud comparable in age to the ovary shown in Fig. 9 (semi-diagrammatic); approximate levels of Figs. 10-16 are marked in Fig. 9. × 27.



FIGS. 19-27 — (*ft*, fibrous thickenings; *ta*, tapetum; *vb*, vascular bundle). Fig. 19. L.s. young anther (semidiagrammatic). × 25. Fig. 20. Enlargement of portion marked 'X.' × 240. Fig. 21. T.s. anther at tetrad stage (semidiagrammatic). × 130. Fig. 22. Portion marked 'Y' showing tetrahedral and decussate tetrads. × 240. Figs. 23-26. Tapetal cells. × 410. Fig. 27. Dehisced anther; fibrous thickenings are also present in the cells of the partition wall between the pollen sacs. × 130.



FIGS. 28-39 — Figs. 28-30. Microspore mother cells; Meiosis I. × 650. Figs. 31-34. Meiosis II. × 650. Fig. 35. Cytokinesis. × 650. Fig. 36. Tetrahedral tetrad. × 650. Figs. 37, 38. Uninucleate and 2-celled pollen grains. × 650. Fig. 39. Palynogram of acetolyzed pollen grain. × 650.

each of the microspores touches one of the arms of the adjacent microspore. During the enlargement of the microspores the mucilaginous wall is absorbed, the original wall of the mother cell breaks down and the microspores are set free. The microspores are triradiate with three slightly curved arms having a concavo-convex outline (Fig. 37).

The microspore has an exine which is thicker in the middle and thinner towards the arms, and a uniformly thin intine (Figs. 38, 39). Each arm has two longitudinal furrows, one on each surface, running from the tip to the centre where they meet. During maturation the central region of the pollen grain becomes broader (Figs. 38, 39).

The microspore nucleus divides to form a larger vegetative and a smaller generative nucleus (Fig. 38). The latter develops a cytoplasmic sheath around it and migrates into one of the arms. The pollen is shed at the 2-celled stage.

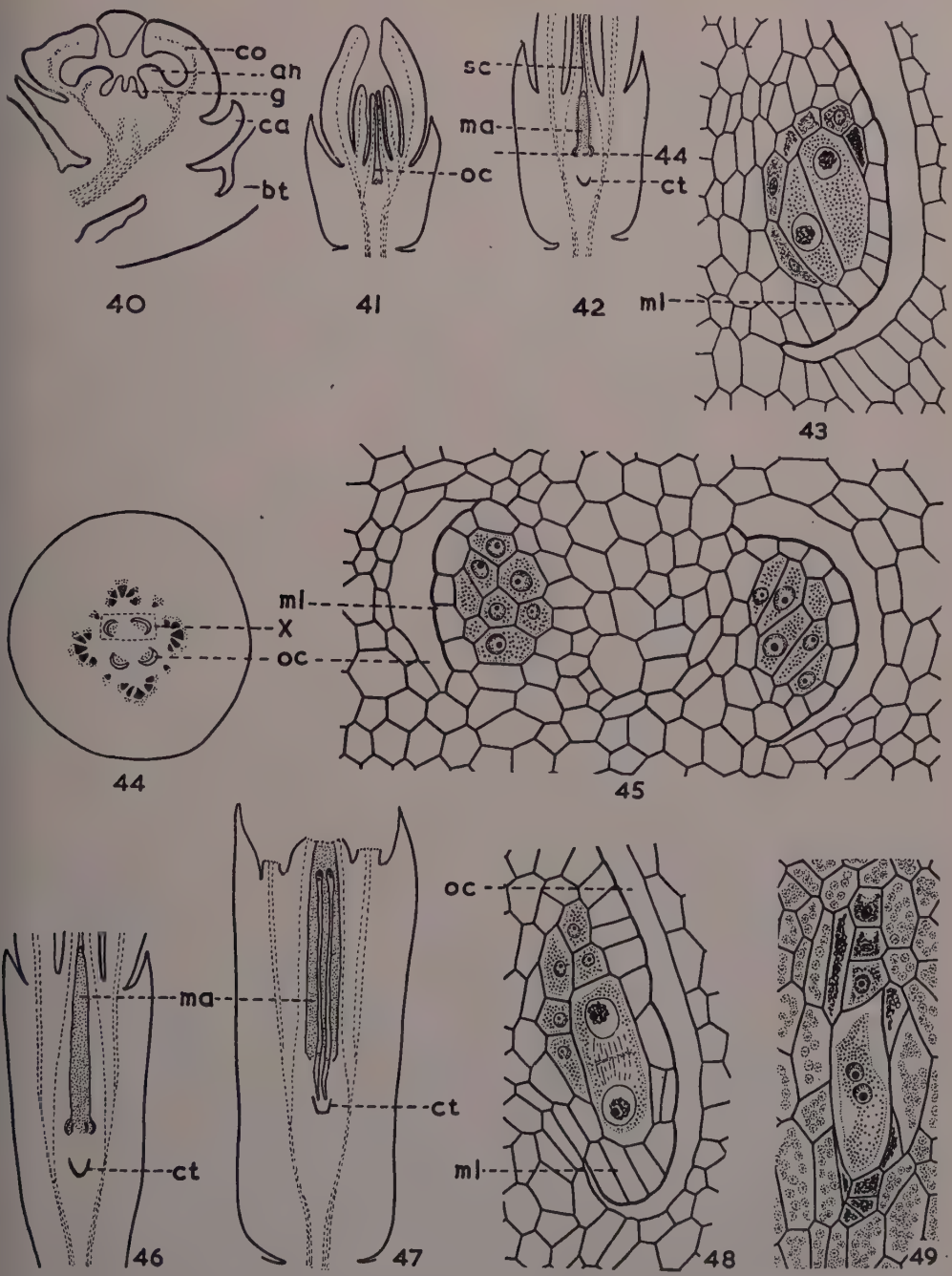
MAMELON — The ovary lacks normal ovules and a longisection of a young bud shows a small mound-shaped projection, the mamelon, at the base of the ovarian cavity (Figs. 41, 42). A few layers below it differentiates a collenchymatous tube (Fig. 42). In the beginning the ovary is unilocular and the base of the mamelon is unlobed. However, before the sporogenous tissue differentiates, the mamelon shows active growth at four points and becomes basally 4-lobed (Fig. 42). In between the lobes, the mamelon fuses with the ovary wall so that the ovary appears tetralocular[3] (Figs. 44, 45). Simultaneously the upper portion of the mamelon elongates and its tip comes to lie at the base of the style (Figs. 42, 46). In open flowers the mamelon measures about 2 mm in length and its boundary becomes obscured except in the basal region.

MEGASPOROGENESIS AND FEMALE GAMETOPHYTE — In each lobe of the mamelon one or two hypodermal layers differentiate into sporogenous cells (Fig. 45). The latter function directly as megaspore mother cells and some of them enlarge appreciably (Fig. 43).

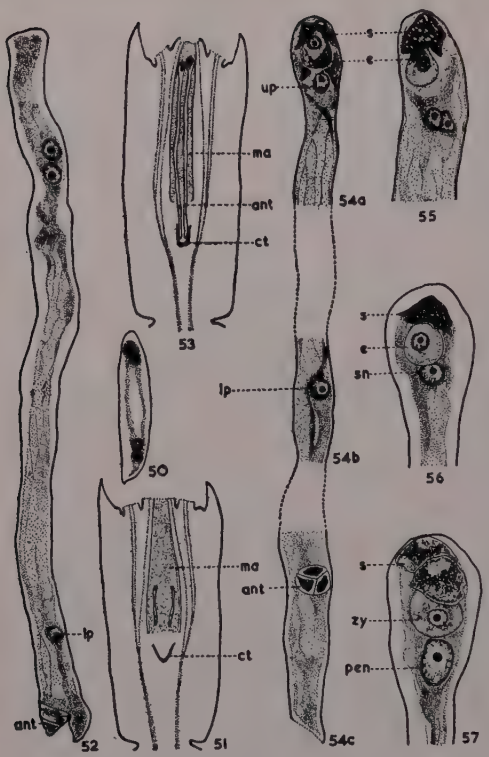
The megaspore mother cell undergoes normal meiosis producing a linear tetrad (Figs. 48, 49). At this time the cells of the mamelon and the ovarian tissue just below it accumulate considerable quantity of starch (Fig. 49).

The 'basal' megaspore of the tetrad develops into 2 and 4-nucleate embryo sacs (Figs. 49, 50). Elongation of the

3. Narayana (1958a) reports a 4-lobed mamelon and a completely chambered ovary in *Lysiana exocarpi*. He points out that the stylar canal is present only in the upper half of the style while the lower half shows four ridges which are at first continuous with the four transverse partitions of the ovarian cavity but later completely obliterate the stylar canal. He also concludes that the mamelon reaches only up to the base of the style. However, in his Fig. 17 (*see* Narayana, 1958; page 148) he has shown a small projection in the middle of the style and it seems likely that in *Lysiana* the tip of the mamelon does extend up to this place. A similar extension of the mamelon up to about 3·5 mm of the 14 mm long style has been reported by Dixit (1958) in *Lepeostegeres gemmiflorus*.



FIGS. 40-49 — (*an*, androecium; *bt*, bract; *ca*, calyculus; *co*, corolla; *ct*, collenchymatous tube; *g*, gynoecium; *ma*, mamelon; *ml*, lobe of mamelon; *oc*, ovarian cavity; *sc*, stylar canal). Fig. 40. L.s. young bud. × 17. Fig. 41. Same; older stage showing differentiation of young mamelon. × 17. Figs. 42, 46, 47. Development stages of mamelon; its tip reaches only up to the base of the style. × 17. Fig. 43. Enlargement of a single lobe of mamelon from Fig. 42 to show megaspore mother cells. × 475. Fig. 44. T.s. ovary at level marked 44 in Fig. 42; note the four lobes of the mamelon. × 35. Fig. 45. Enlargement of portion marked 'X'. × 475. Figs. 48, 49. Dyad and tetrad stages; in Fig. 49 the upper three megaspores have degenerated while lowest megaspore shows two nuclei. × 475.



FIGS. 50-57 — Figs. 50, 51 and 53 from microtome sections, rest from dissected whole mounts (*ant*, antipodal cells; *ct*, collenchymatous tube; *e*, egg; *lp*, lower polar nucleus; *ma*, mamelon; *pen*, primary endosperm nucleus; *s*, synergid; *sn*, secondary nucleus; *up*, upper polar nucleus; *zy*, zygote). Fig. 50. 4-nucleate embryo sac. × 153. Figs. 51, 53. Longisections of ovaries at 6-nucleate and mature embryo sac stages (semidiagrammatic). × 10. Fig. 52. Whole mount of a 6-nucleate gametophyte. × 153. Figs. 54a-c. Upper, middle and lower portions of a mature embryo sac. × 153. Fig. 55. Tip of gametophyte, the polar nuclei are lying close to each other. × 153. Fig. 56. Same; showing egg apparatus and secondary nucleus. × 153. Fig. 57. Fertilized embryo sac. × 153.

gametophyte commences at the 4-nucleate stage and the lower nuclei divide earlier resulting in a 6-nucleate condition (cf. Maheshwari & Singh, 1952; Narayana, 1958a). The lower quartet forms the three antipodal cells and the lower polar nucleus (Figs. 51; 52; 54b, c). The four daughter nuclei produced by the division of the two nuclei in the upper end of the embryo sac organize into the egg apparatus and the upper polar nucleus (Figs. 53, 54a). The tips of the embryo sacs are somewhat dilated and they extend only up to the base of the style (Figs. 47, 53). Their lower ends elongate into caeca which penetrate the underlying tissues reaching almost up to the collenchymatous tube (Fig. 53). The antipodal cells are left *in situ* (Figs. 52, 54c). The total length of the embryo sacs (including the chalazal caeca) is approximately 2 mm. Usually four embryo sacs, one in each lobe of the mamelon, develop concurrently and attain more or less the same length (Fig. 53). The difficulty of tracing the entire embryo sac in sections was overcome by studying dissected whole mounts.

The upper polar nucleus lies appressed to the egg (Fig. 54a). Polar fusion takes place below the egg apparatus (Fig. 55) and the secondary nucleus remains there until fertilization (Fig. 56).

Double fertilization has not been observed but it is presumed to be normal.

ENDOSPERM — The primary endosperm nucleus (Fig. 57) migrates to the chalazal caecum (situated in the collenchymatous tube) where further development takes place. The earliest stage available in the material at my disposal was an 8-celled, 2-seriate endosperm (Fig. 61). It extends from the base upwards and becomes 4-seriate (Fig. 62). Stages in the fusion of different endosperms developing in the same ovary were not observed but older ovaries showed only a single endosperm (Figs. 65-67) and there is no doubt that a composite endosperm is formed as usual.

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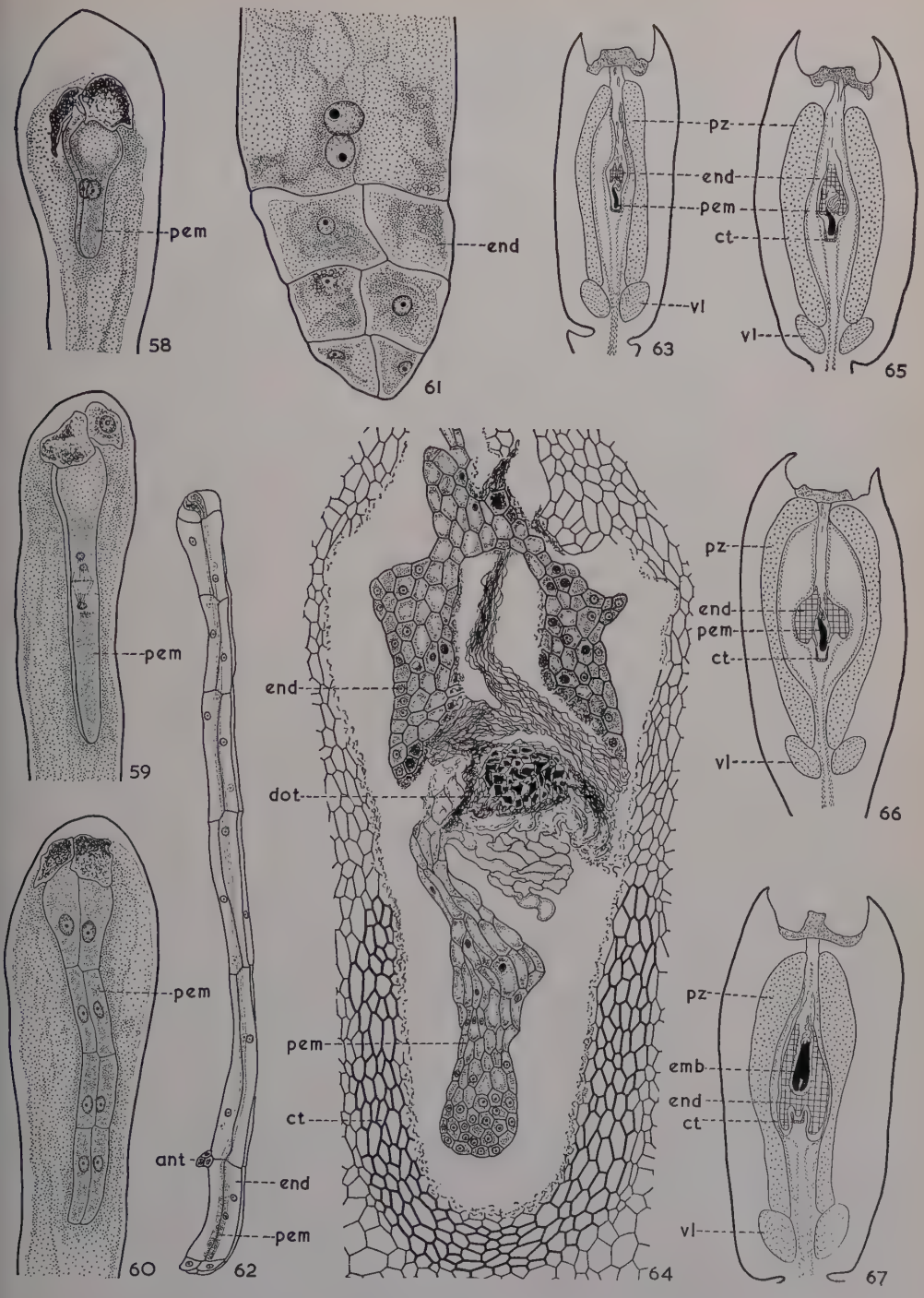
FIGS. 58-67 — Figs. 63-67 from microtome sections, rest from dissected whole mounts (*ant*, antipodal cells; *ct*, collenchymatous tube; *dot*, degenerated ovarian tissue; *emb*, embryo; *end*, endosperm; *pem*, proembryo; *pz*, parenchymatous zone; *vl*, viscid layer). Fig. 58. Two-celled proembryo. × 273. Figs. 59, 60. Four and 8-celled proembryos. × 273. Fig. 61. Basal end of embryo sac showing 8-celled endosperm (the wall of the uppermost cell is in the plane of paper). × 274. Fig. 62. Endosperm and biseriate proembryo; note the remnants of persistent antipodal cells. × 80. Fig. 63. L.s. young fruit (semidiagrammatic). × 10. Fig. 64. Enlargement of composite endosperm and globular embryo with multiseriate suspensor. × 115. Figs. 65-67. L.s. fruits showing developmental stages of endosperm and embryo (semidiagrammatic). × 10.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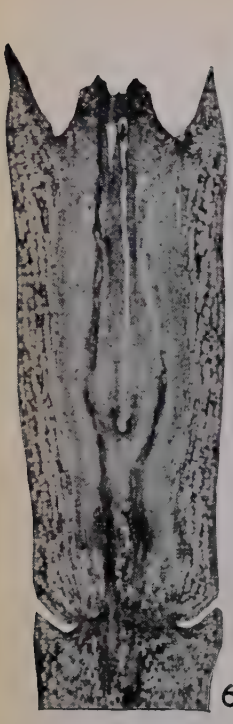
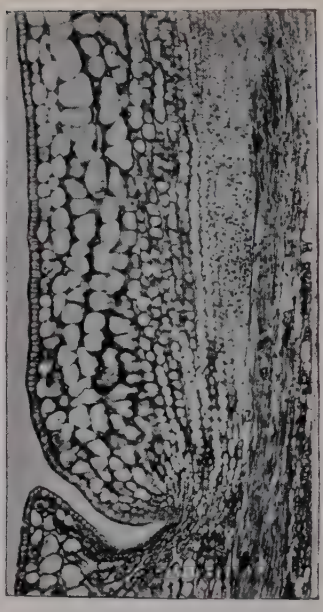
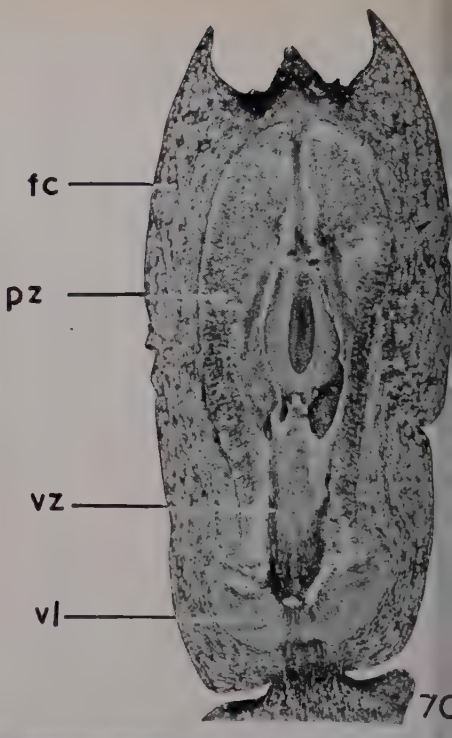
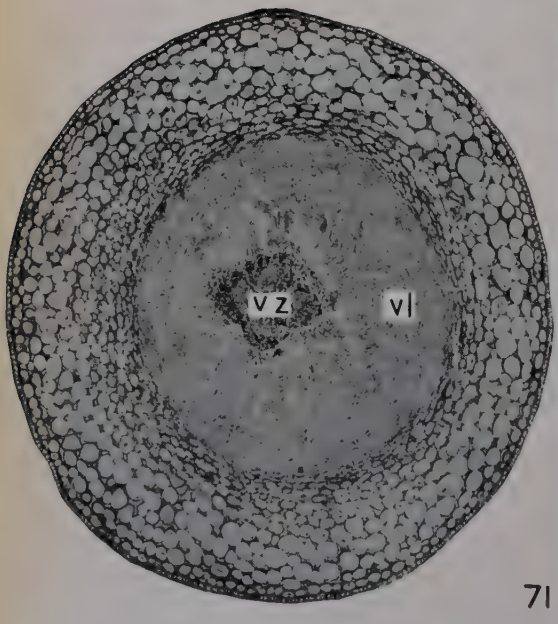
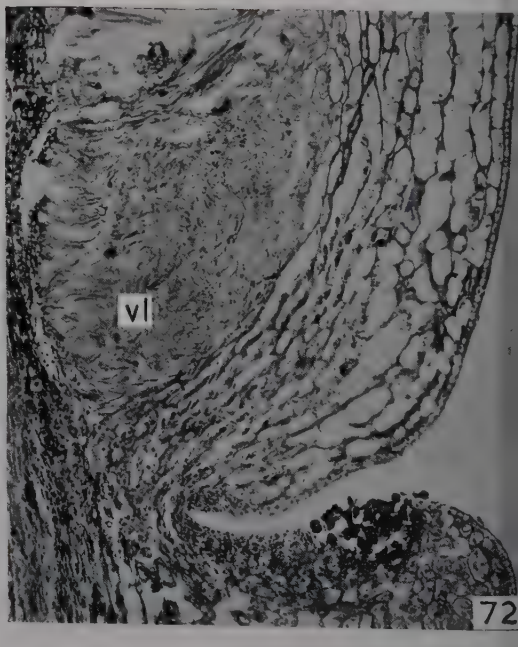
FIGS. 58-67.











FIGS. 68-72 — Photomicrographs (*fc*, fleshy coat; *pz*, parenchymatous zone; *vl*, viscid layer; *vz*, vascular zone). Fig. 68. L.s. ovary at mature embryo sac stage. × 16. Fig. 69. Enlargement of a portion of lower part of the ovary. × 48. Fig. 70. L.s. nearly mature fruit; note that the viscid layer is restricted only to the basal region. × 13. Fig. 71. T.s. ovary through viscid layer. × 36. Fig. 72. Enlargement of pericarp at the level of viscid layer from Fig. 70. × 48.

EMBRYO — The zygote shows characteristic vacuolation. It elongates considerably and undergoes a vertical division (Fig. 58) followed by transverse divisions resulting in a biseriate proembryo (Figs. 59, 60). Due to elongation of the suspensor cells the proembryo traverses through the 4-seriate endosperm (Fig. 62). Eventually it grows beyond the endosperm and comes to lie in the collenchymatous tube. Now the terminal embryonal tier and the adjacent cells undergo repeated divisions forming a broad fleshy suspensor and a club-shaped embryonal mass (Figs. 63, 64). Although three or four proembryos are initiated in each ovary, only one of them reaches maturity. The proembryonal mass lying below the endosperm is gradually pulled up (probably due to coiling and twisting of the suspensor cells — *see* Maheshwari & Singh, 1952). The growth of the endosperm in the basal portion also assists in this process and the embryonal mass is thus shifted to a more central position in the endosperm (Figs. 65-67). Further growth of the densely staining embryonal mass produces the heart-shaped and finally the dicotyledonous embryo (Fig. 67).

FRUIT — At first the ovary wall is uniformly parenchymatous (Figs. 68, 69) but after fertilization it differentiates into four distinct zones: an outer fleshy coat, a parenchymatous zone, a viscid layer and the region of the vascular tissue (Fig. 70).

The fleshy coat consists of parenchymatous cells interspersed with sclereids. The latter show a wide lumen and broad pit canals. In the upper and middle portions of the fruit the fleshy coat is followed by a parenchymatous zone of large, vacuolate cells (Fig. 70).

At the club-shaped stage of the proembryo the cells at the base of the fruit, next to the fleshy coat, elongate radially, become greatly coiled and twisted and show scanty cytoplasm and flattened nuclei. This tissue constitutes the viscid layer (Figs. 71, 72) and, unlike other Loranthaceae, it is limited only to the base of the fruit (*see* Dixit, 1958). In the region of the viscid layer the parenchymatous zone is absent so that the former directly surrounds the innermost vascular zone (Figs. 70-72).

In the mature fruit the endosperm is 4-lobed and its basal portion encloses the collenchymatous tube (Fig. 70). The food reserve in the endosperm is mainly starch.

The mature embryo is 3-4 mm long and except for the apical portion it is completely embedded in the endosperm. Its radicular end shows typical endarch collateral bundles and represents the hypocotyledonary extension rather than true radicle. The cotyledons remain apart throughout their length.

Summary and Conclusion

The morphology and embryology of *Peraxilla tetrapetala* has been investigated. The flowers are bisexual, actinomorphic and polypetalous. The calyculus is rimmed and is devoid of a vascular supply.

The anther wall consists of the epidermis, fibrous endothecium, one or two middle layers, and glandular tapetum. The adjacent locules of the anther do not fuse but dehisce independently while the bud is still closed. Some of the cells of the partition wall separating the two sporangia also acquire fibrous thickenings. Tetrahedral and decussage tetrads are formed and the pollen grains are triradiate. Shedding occurs at the 2-celled stage.

The ovary is basally tetralocular and the mamelon is basally 4-lobed, each lobe representing a reduced ovule. A collenchymatous tube differentiates several layers below the mamelon.

Several sporogenous cells differentiate hypodermally in each lobe of the mamelon and directly function as megaspore mother cells. The tetrads are linear and usually the 'basal' megaspore develops further.

A 6-nucleate stage precedes the 8-nucleate gametophyte. Four or five embryo sacs develop in an ovary and their extension is limited up to the base of the style. The chalazal end extends into a caecum leaving the antipodal cells *in situ*.

The endosperm is Cellular and finally becomes 4-lobed.

The first division of the zygote is vertical and further divisions are transverse resulting in a long biseriate proembryo. Out of the several proembryos developing in

an ovary, usually one reaches maturity. The mature embryo is dicotyledonous and lacks a true radicle.

The pericarp is distinguishable into four zones but the viscid layer is restricted only to the base of the fruit.

Peraxilla shows basifixed anthers, tetralocular ovary with a basally 4-lobed mamelon, tips of embryo sacs not extending beyond the base of style, lobed endosperm and a baccate fruit-features characteristic of the Elytranthinae. Therefore, on embryological grounds, its inclusion in the subtribe Elytranthinae, tribe Elytrantheae (Danser, 1933) is fully justified.

I am greatly indebted to Dr B. M. Johri and Professor P. Maheshwari for comments and valuable suggestions.

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WILLEELLA ORDINATA BÖRGESEN FROM CAPE COMORIN, SOUTH INDIA

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The genus *Willeella* was established by Börgesen (1930) for a marine green alga from Okha Port which was named by him as *W. ordinata* gen. et sp. nov. Since then two other species of this genus have been described, one *W. japonica* by Yamada and Segawa (Segawa, 1938) from Japan and the other *W. mexicana* by Dawson (1950) from the Pacific coast of Mexico. During a visit to Cape Comorin in South India, the writer collected some material of *Willeella ordinata* Börgs. and an account of some aspects of the alga is given here below.

Börgesen (1930) has already given a detailed account of the structure of the

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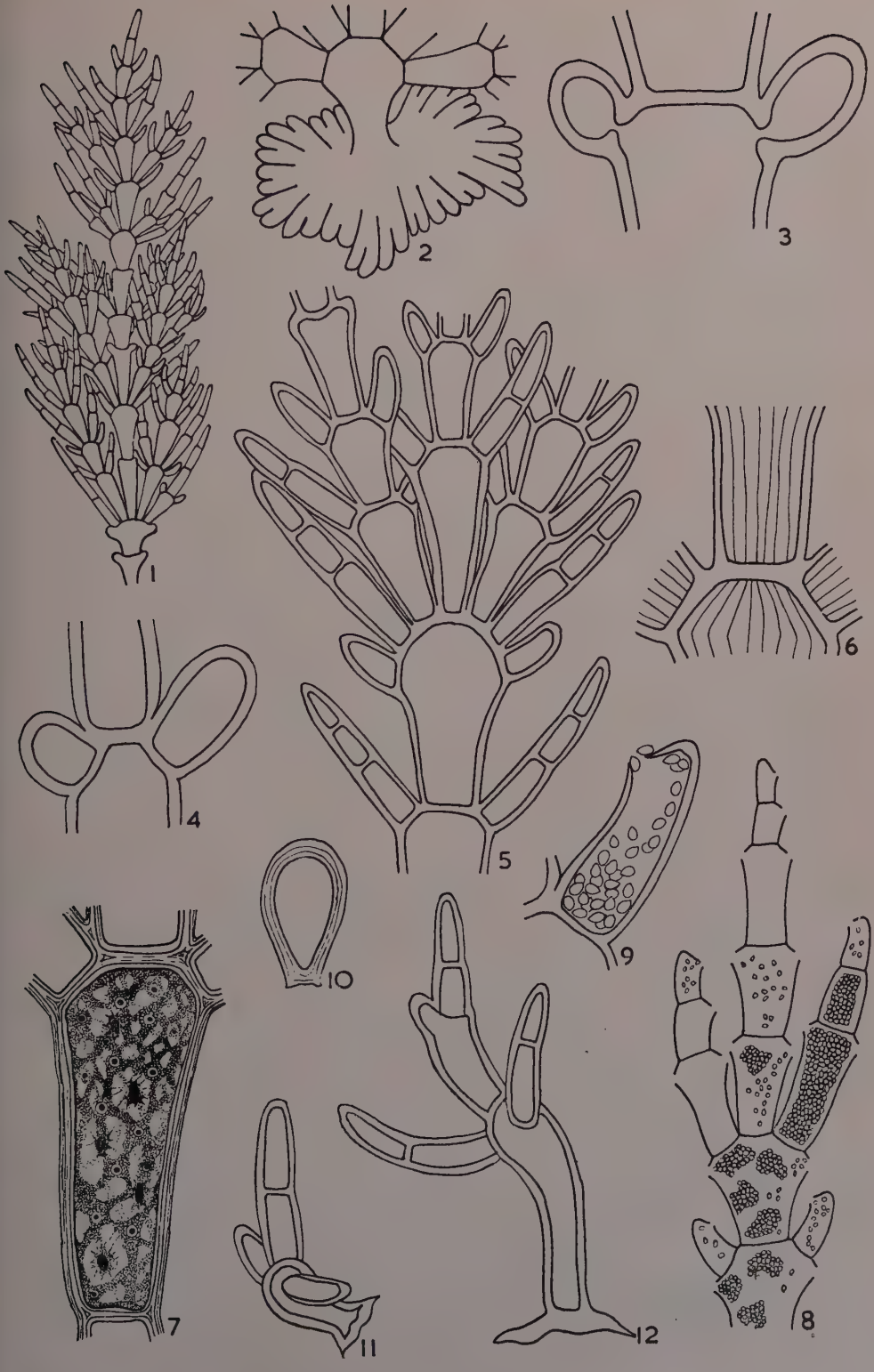
Figs. 1-12 — Fig. 1. A part of a frond to show the general habit. × 16. Fig. 2. Hapteroid basal cell. × 55. Fig. 3. Initiation of laterals. × 250. Fig. 4. Lateral initials separated by septa. × 250. Fig. 5. Part of a frond showing the mode of branching. × 75. Fig. 6. A cell of the thallus showing striations on the cell-wall. × 250. Fig. 7. A single cell showing details of structure. × 250. Fig. 8. Part of a frond showing sporangia. × 75. Fig. 9. A single sporangium with escaping swarmers. × 250. Figs. 10-12. Germlings in various stages. × 250.



FIGS. 1-12.

thallus in this alga. Later he also described some fertile material from the same collection (Börgesen, 1934). The writer's observations on the Cape Comorin alga largely confirm Börgesen's earlier account. A more detailed account of the alga, especially its cell structure and its swarmspores, and also an account of its germlings are given in this paper.

The alga grows in clusters (Fig. 13) on rocks which are partially exposed during low tide. The plant is attached to the substratum by a basal hapteroid cell (Fig. 2). The main axis is composed of cylindrical cells which are gradually tapering towards their upper end. Growth of the axis is apical by means of a bluntly pointed terminal cell. The apical cell, by a series of transverse divisions, gives rise to a succession of segments which together make up the main axis. Formation of laterals takes place from the upper ends of the axial cells commencing from the third cell from the top (Fig. 1).

At each node the laterals are initiated as a knob-like or round protuberance on either side at the upper end of the axial cell (Fig. 3). The contents of the protuberance are then separated by a cross-wall and the cell so formed gives rise to the lateral (Fig. 4). After the formation of one pair of laterals in this manner, a second pair is developed from the same cell just below the first pair (Fig. 5). Subsequently a third pair is formed below the second pair. All the laterals thus formed lie in one plane and are spread out in a fan-like manner (Figs. 5, 14-16).

Though the growth of the alga is mainly apical, the older cells of the main axis after some time divide transversely into two cells by intercalary division. The lower of these two cells gives rise to a pair of small laterals from its upper end (Fig. 5). Börgesen (1930, p. 156) says " From the upper end of the cells in the main branches opposite branches are given off. Every other of these pairs of branches are small and dwarfish and composed as a rule of a single cell and sometimes of a few cells and generally not ramified (Fig. 4a)." Börgesen evidently did not recognize the later intercalary transverse division of the older cells of the main axis into two and the formation of lateral branches by the lower of these two cells; hence his statement that " every other of these pairs of branches are small and dwarfish ". But Papenfuss & Egerod (1957, p. 83) recognized in their South African material of the alga the occurrence of this intercalary transverse division in the cells of the main axis. They have, however, made a mistake in stating, " the only difference between the plants from South Africa and India lies in the fact that in those from South Africa, the cells in the main axis occasionally undergo intercalary transverse division, and the newly formed segments in turn produce opposite branches at the distal end ". If they had examined Börgesen's figures carefully (1930, Fig. 4a, b), they would have seen the occurrence of intercalary transverse division in the Indian alga also. In Börgesen's Fig. 4a, it is seen that the original sixth cell from the apical end has undergone intercalary transverse division into two cells. Again, the original seventh cell from the apical end has divided into two by intercalary transverse division and two short opposite branches have already been formed from the distal end of the lower cell. The same process is repeated downwards. Unfortunately, Papenfuss & Egerod have not given any figures of their African alga. But as far as one could gather from their description of the alga, it is very clear that the African alga in no way differs from the Indian alga.

The cell-wall is rather thick and lamellate and shows longitudinal striations (Fig. 6). These striations are most pronounced in older cells. The chloroplast

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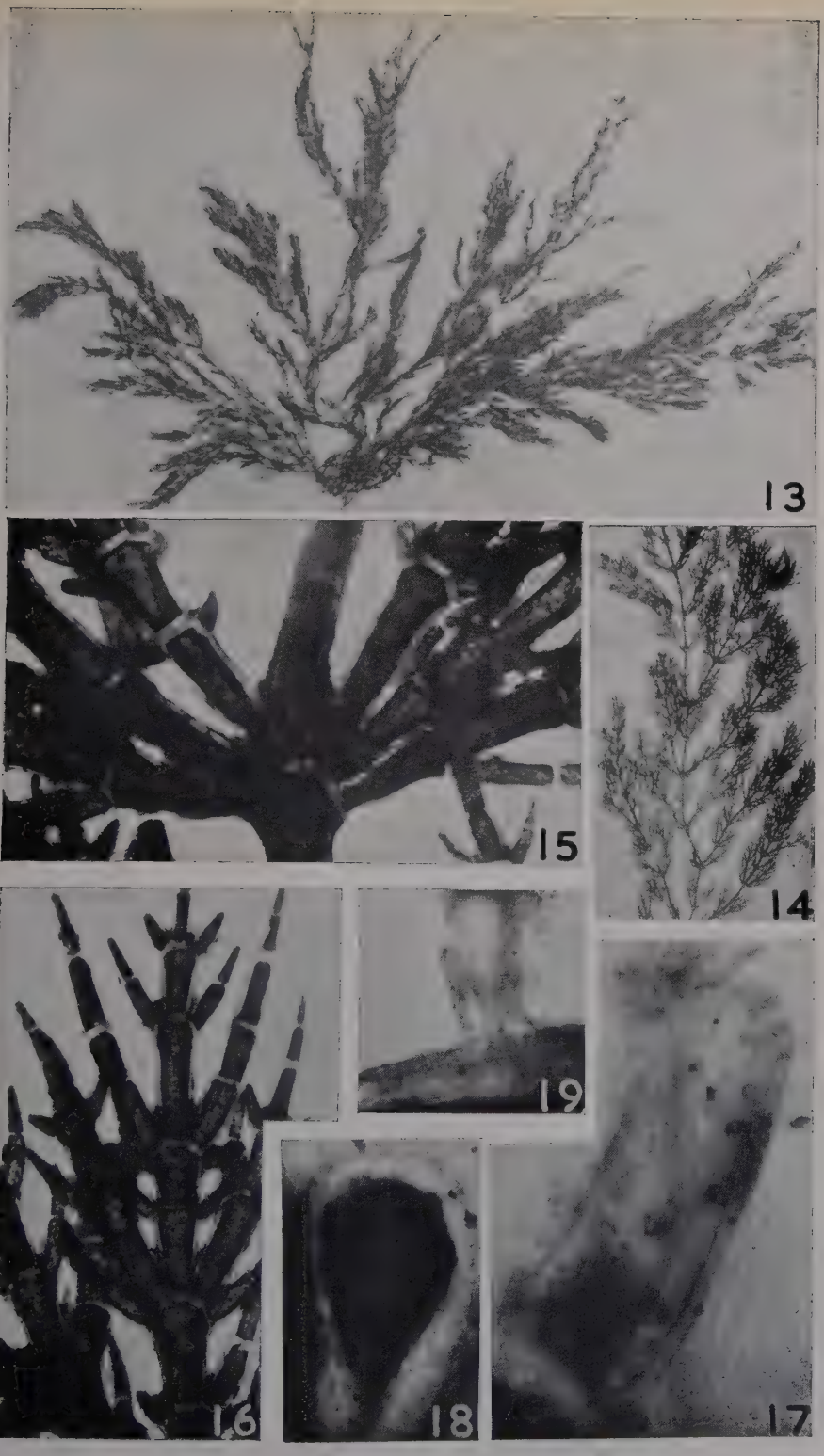
FIGS. 13-19 — Fig. 13. Habit (from herbarium specimen). × Natural size. Fig. 14. A portion of the thallus. × 10. Figs. 15, 16. Parts of a frond to show details of the branching. × 50. Fig. 17. A sporangium with swarmers escaping (same as Fig. 12). × 500. Fig. 18. A one-celled germling. × 500. Fig. 19. Hapteroid basal part of a germling. × 500.



FIGS. 13-19.

is reticulate and includes several pyrenoids. There are four to eight nuclei in the cell (Fig. 7).

Börgesen (1934) described some fertile material from Okha Port and gave a figure of the end portion of the thallus, showing empty cells with apical or sub-apical openings in the cell-walls. He assumed, quite correctly, that these empty cells were zoosporangia. In the Cape Comorin material also, the writer observed a number of such empty cells with apical or sub-apical openings. But in a number of such cells he found a number of rounded or oval bodies also (Figs. 8, 9, 17). These bodies are clearly swarmspores of the alga which had not escaped outside.

A few germlings of the alga were found growing attached to the branches of the mature alga. The youngest germling was unicellular and claviform or obpyriform in shape (Figs. 10, 18). An older germling (Fig. 11) had a small axis consisting of an elongate, more or less cylindrical basal cell with a hapteroid lower end (Fig. 19) and an upper cell. The basal cell had already produced at its distal end two one-celled laterals. A still older germling (Fig. 12) showed the characteristic branching of the alga.

A word may be said at this place regarding *W. mexicana* Dawson. Papenfuss & Egerod (1957) have expressed a doubt regarding the validity of this species. They state that the Mexican alga does not differ materially from *W. ordinata* Börgs. But the description and figure given by Dawson of the Mexican alga are quite characteristic. It differs from the Indian alga in the shape of its cells, in its general habit, in the irregularity in the production of its laterals, and in the late formation of the cross-walls separating the laterals. In view of these features, the writer thinks that Dawson's Mexican alga is quite a distinct species and not the same as *W. ordinata*.

The writer is grateful to Prof. M. O. P. Iyengar for his valuable suggestions in the preparation of this paper.

Post-script: Since sending the above to the press, the writer has seen the paper by Dawson (1959) entitled " Marine algae from the 1958 cruise of the Stella Polaris in the Gulf of California ", Los Angeles County Mus. Contrib. Sci. 27 : 1-39. Dawson tentatively refers his *Willeella mexicana* to *Cladophoropsis* ? *robusta* Setch. & Gard. He also cites a number of points of difference between this and *W. ordinata* Börgs. and indicates that his alga is more related to *Valoniopsis* than to *Willeella*. Figure 3A in his paper is a photograph of some specimens of *Cladophoropsis robusta* and it is clear that contrary to what has been stated by Papenfuss & Egerod (1957) it is not the same as *W. ordinata* Borgs. The writer is thankful to Dr Yale Dawson for kindly directing his attention to the above paper.

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MORPHOLOGICAL AND EMBRYOLOGICAL STUDIES IN THE FAMILY SANTALACEAE— V. *OSYRIS WIGHTIANA** WALL.

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Investigations on *Osyris* are confined to three species, namely *O. alba* (Van Tieghem, 1869; Guignard, 1885; Schaeppi & Steindl, 1937; Smith & Smith, 1942), *O. arborea* (Rao, 1942; Paliwal, 1956) and *O. nepalensis* (Griffith, 1843). On the basis of ontogenic and morphological studies, Schaeppi & Steindl (1937) concluded that the ovary is embedded in the tissue of the receptacle. Smith & Smith (1942) furnished anatomical evidence in favour of the receptacular nature of the inferior ovary. Paliwal (1956) states that in *O. arborea* it is receptacular below and appendicular above.

Griffith, Guignard, Schaeppi & Steindl and Rao believe that the ovule comprises only the nucellus and is 'naked', the integument being eliminated. According to Paliwal, on the other hand, it is the nucellus and not the integument which has undergone reduction.

The development of the male and female gametophytes, endosperm and embryo is more or less similar in *O. alba* (Guignard, 1885; Schaeppi & Steindl, 1937) and *O. arborea* (Rao, 1942; Paliwal, 1956). Owing to the incomplete nature of the earlier accounts the embryology of *O. wightiana* has been reinvestigated.

Material and Methods

The material was obtained through the courtesy of Father L. M. Balam, Dr S. P. Bhatnagar, Professor P. Maheshwari, Dr H. Y. Mohan Ram, Mr M. P. Nayar and Dr (Mrs) Vimla Vasil, and was mostly collected from Khandala, Lonavala, Nandi Hills, Nilgiris, Ootacamund, Poona and Tiruchirapalli. I am very grateful to all these persons for their help.

The ethyl alcohol-tertiary butyl alcohol series was used for the dehydration of the material and before processing the fruits were softened in 10 to 20 per cent hydrofluoric acid in 70 per cent ethyl alcohol. Sections were cut 5 to 20 microns thick and stained with safranin and fast green. For tracing the course of the pollen tubes and the development of the endosperm and embryo, the fertilized ovaries were pretreated with 5 per cent potassium hydroxide at 40°C for 24 hours. These were then dissected and whole mounts prepared in a mixture of glycerine and acetocarmine.

Observations

Floral Morphology — The flowers of *Osyris wightiana* are either male (Figs. 1-3) or female (really male-sterile) (Figs. 4-6). The short-stalked male flowers are borne in axillary clusters forming short panicles (Figs. 1, 2). The female flowers are much larger, pedicellate, solitary and axillary (Figs. 4, 5). Occasionally, twin flowers may develop (Fig. 6). The male as well as female flowers have a closely appressed bract and two bracteoles which fall off quite early (cf. Paliwal, 1956).

The floral organs develop in acropetal succession and the primordia of the perianth are followed by those of the androecium and gynoecium (Figs. 7-9). As the carpels grow they enclose a small cavity where the central placentum develops simultaneously. This gradually acquires

**Osyris wightiana* Wall. Syn. *O. arborea* Wall. (*see* Santapau, 1953).

FIGS. 1-20 — Floral morphology (*a*, androecium; *g*, gynoecium; *h*, hair; *p*, perianth; *pc*, placental column; *ov*, ovule; *rg*, rudimentary gynoecium). Fig. 1. Flowering twig, male. × 1. Fig. 2. Longisection, male inflorescence. × 11. Fig. 3. Male flower. × 5. Fig. 4. Flowering twig, female. × 1. Fig. 5. Female flower, part of perianth removed to show the floral organs. × 5. Fig. 6. Twin flowers. × 5. Figs. 7-10. Successive stages in the development of female flower. × 83. Figs. 11-15. T.s. female flower at levels marked 11-15 in Fig. 10. × 16. Fig. 16. Longisection of male flower showing hairs at the base of the perianth lobe (left). × 25. Fig. 17. Enlarged view of hair and adjacent cells from Fig. 16. × 250. Figs. 18-20. T.s. male flower at levels marked 18-20 in Fig. 16. × 16.

a dome-shaped appearance and bears three, occasionally four, anatropous ovules (only two ovules are seen in Fig. 10). The development is similar in the male flowers but the growth of the gynoecium is arrested (Fig. 16).

The male as well as female flowers have three (rarely four) perianth lobes (Figs. 13-15, 18-20) which are united at the base (Figs. 13, 14, 18) but are free at the tip (Figs. 15, 19, 20). There are three epiphyllous stamens (Figs. 14, 18). An angular disc is present in between the stamens of both male and female flowers (Figs. 14, 15 from female, and Figs. 18, 19 from male flowers). The male flowers show glandular hairs at the bases of the stamens which arise from the epidermal cells of the perianth (Figs. 16, 17). Rao (1942) stated that glandular hairs are present both in the male and female flowers of *Osyris arborea* but, according to Paliwal (1956), these hairs develop only in male flowers which is in conformity with my observations. Paliwal further pointed out that in this species the female flowers have a polyphyllous perianth and free stamens at the 'top of the ovary'. On the basis of comparative study he concluded that in the female flowers the gamophyllous part of the perianth has fused with the ovary for a considerable distance and as a result thereof the perianth appears to be polyphyllous. This does not seem to be true since the gamophyllous and epiphyllous conditions are quite apparent.

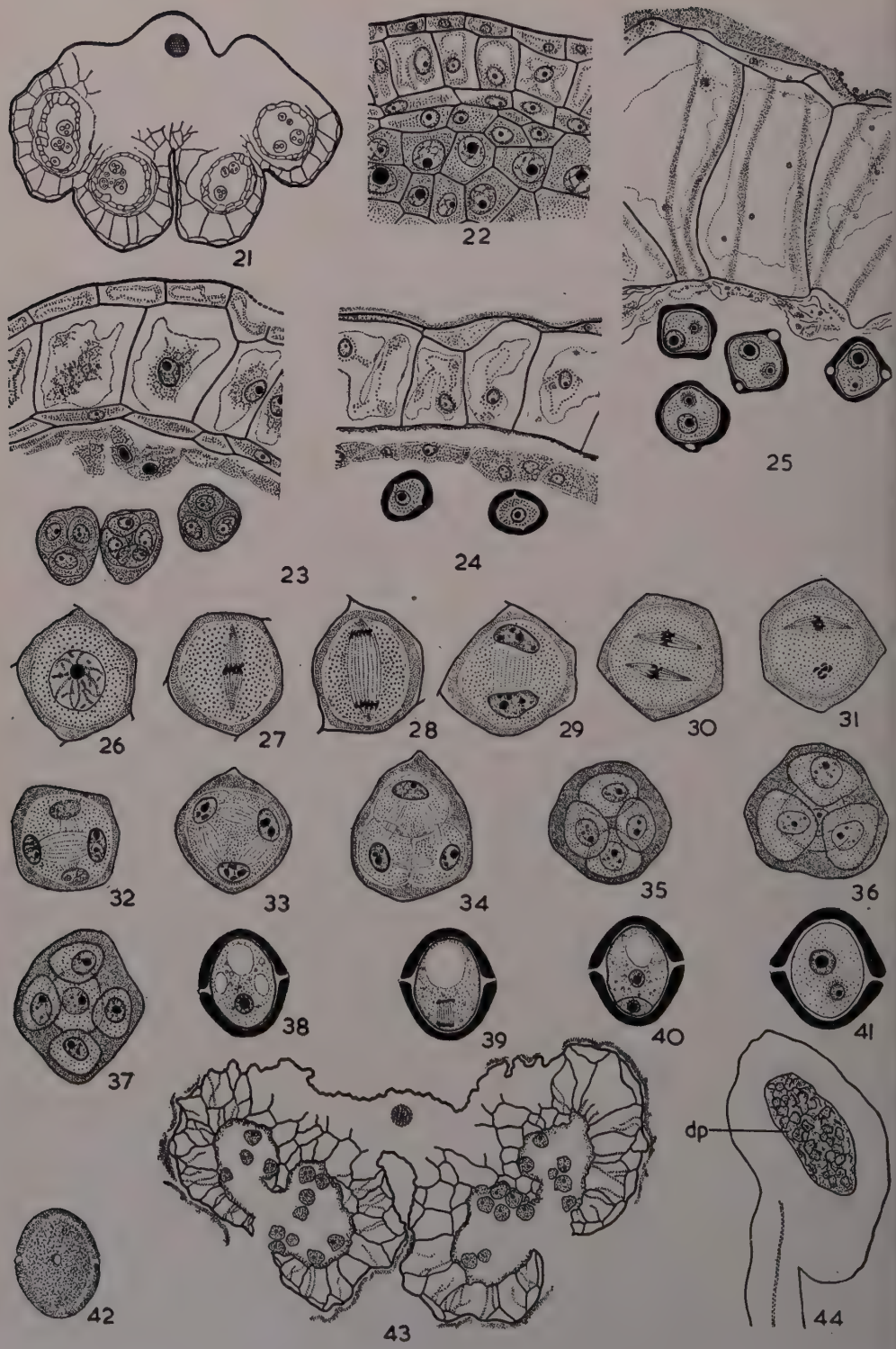
The gynoecium is tricarpellary and syncarpous. The ovary is inferior and in transverse sections it appears trilocular below (Fig. 11) and unilocular above (Fig. 12). A distinct strand composed of small cells traverses the central part of the flower below the ovarian cavity (Fig. 10) (*see* also Paliwal, 1956). The short thick style has a narrow stylar canal and terminates into three flap-like stigmatic lobes (Figs. 5, 6).

MICROSPORANGIUM — The anther wall comprises the epidermis, endothecial layer, single middle layer and the tapetum (Figs. 21, 22). The thin-walled epidermal cells become tangentially elongated and their outer walls become conspicuously cutinized. The epidermis persists in the mature anther and 'oily' globules appear both on the outer and inner sides. Paliwal (1956) stated that in the female flowers the globules appear only after the degeneration of epidermis.

The endothecial cells elongate radially and develop fibrous thickenings at the uninucleate stage of pollen grains in the female flowers and at the 2-celled stage in the male flowers (Fig. 25). The middle layer collapses at the microspore tetrad stage but its remnants persist until the uninucleate pollen grains are formed (Figs. 23, 24). Sometimes periclinal divisions occur in the tapetal cells. The tapetum is glandular and its cells remain uninucleate throughout. It degenerates during the maturation of the anther (Figs. 23-25). Paliwal noted a beak in the anther and in this region the endothecial cells were more prominent. He also points out that the tapetum becomes 2 or 3-layered, the cells of the inner layer elongate and their protoplasts protrude between the dividing microspore mother cells. However, I did not observe any beak or the protrusion of tapetal cells or protoplasts into the locule.

MICROSPOROGENESIS AND MALE GAMETOPHYTE — Repeated divisions of the sporogenous cells give rise to a large number of microspore mother cells. Prior to meiosis a special mucilaginous wall is secreted between the protoplast of the mother cell and the original wall. The reduction divisions are simultaneous (Figs. 26-32) and during Meiosis II the spindles may lie parallel (Fig. 30) or at right angles (Fig. 31) to each other. Secondary spindles also appear after Meiosis II (Fig. 33). Cytokinesis takes place by furrowing (Fig. 34) and both decussate and tetrahedral tetrads are formed (Figs. 35, 36). Occasionally the 'tetrads' contain five microspores (Fig. 37). The microspore nucleus divides to form a large vegetative and a small generative cell (Figs. 38-41), and shedding occurs at the 2-celled stage. The mature pollen grains are ovoid and have a thin intine and a thick exine showing three germ pores (Fig. 42) (cf. Erdtman, 1952).

The dissolution of the septum between the pollen sacs results in a confluence of the adjacent locules. The disorganization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FIGS. 21-44.

of the narrow strip of thin-walled cells at the junction of the anther lobes brings about dehiscence (Fig. 43).

In the female flowers the anthers degenerate at the microspore mother cell or tetrad stage. Even if development continues further, the pollen grains reach only up to the uninucleate stage (Fig. 44). According to Schaeppi & Steindl (1937) the pollen reaches maturity in the female flowers of *O. alba* but it is not fertile.

Ovule — The ovular primordia arise laterally from the massive dome-shaped placenta and grow downwards reaching up to the base of the ovarian cavity. At this stage the ovules, which show a megaspore mother cell, turn at right angles and commence growing upwards. By the time a megaspore tetrad is formed the ovules become completely anatropous. The curvature is not always in the same direction and may take place both towards or away from the placenta (cf. Paliwal, 1956).

Paliwal (1956) mentions that in *O. arborea* the ovule shows a central nucellar tissue (*see* his Figs. 130, 131) but my preparations did not reveal any distinction between the nucellus and the integument. The cells surrounding the megaspore mother cell undergo both periclinal and anticlinal divisions forming a massive integument. Since it does not grow beyond the tip of the ovule, a micropyle is not formed.

Megasporogenesis and Female Gametophyte — Figure 45 shows three hypodermal sporogenous cells. Usually only one of them enlarges and functions as the megaspore mother cell (Fig. 46). The latter produces a linear tetrad of which the chalazal megaspore develops further (Figs. 47, 48). Figures 48-50 show the 2, 4 and 8-nucleate stages. The synergids are beaked and have a prominent filiform apparatus. The antipodal cells are ephemeral (Figs. 50, 51).

The 4-nucleate embryo sac elongates considerably, destroys the ovular epidermis and its tip comes to lie in the ovarian cavity. A lateral caecum arises from the chalazal end of the gametophyte leaving the antipodal cells *in situ* (Fig. 51). The caecum penetrates the ovular tissue and invades the funiculus and the placental column (Figs. 52, 53). The mature embryo sac is ↳- or ↲ - shaped. Sometimes it may form a loop (Fig. 53). Rao (1942) observed that the chalazal caeca of different embryo sacs fuse in the placental column. With the help of dissected whole mounts I was able to trace the three independent caeca without showing any sign of fusion. Occasionally twin embryo sacs develop in the same ovule.

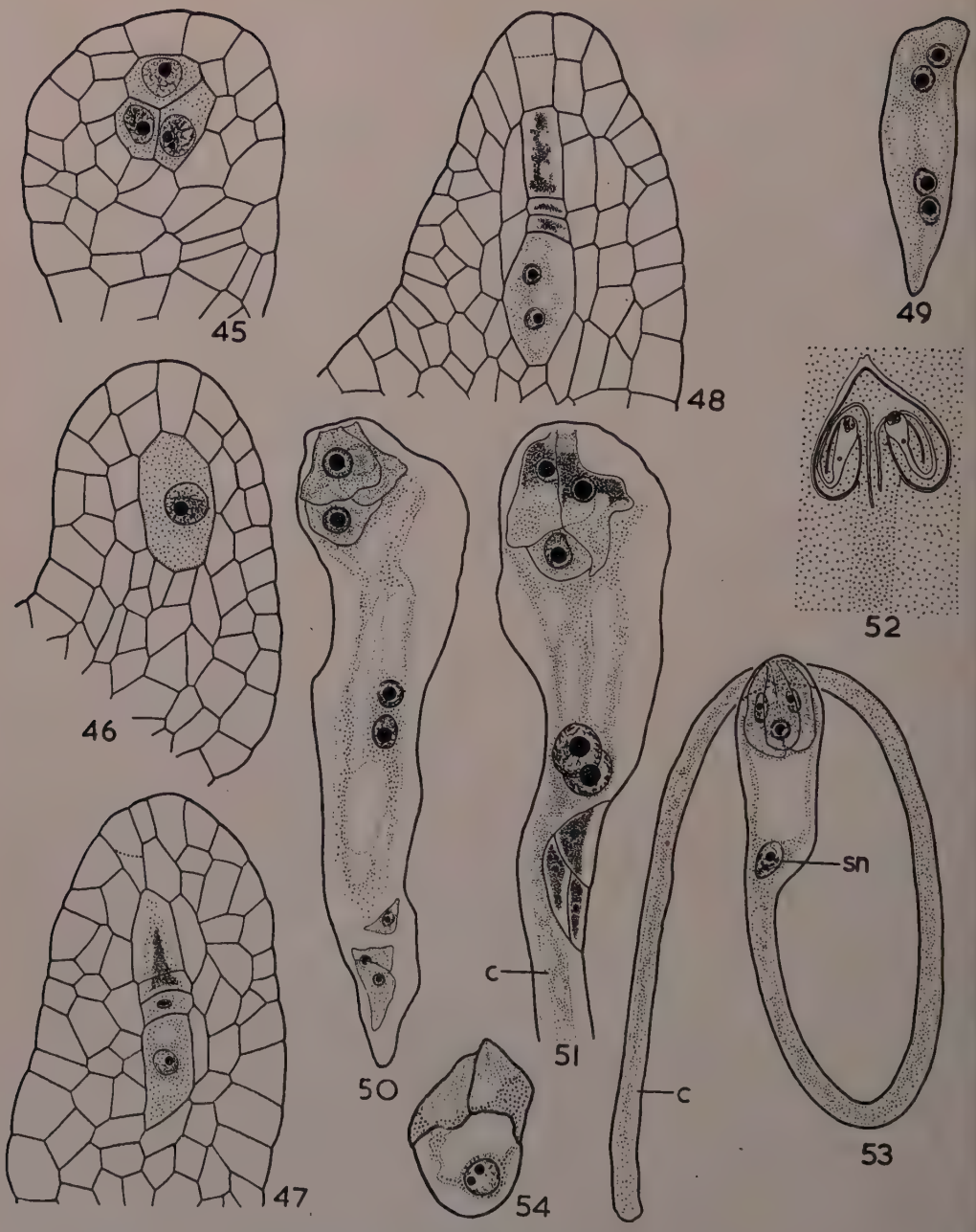
Fertilization — The pollen tubes are persistent as in *Santalum* (Griffith, 1843; Bhatnagar, 1959) and remain attached to the tip of the embryo sac. Both syngamy (Fig. 54) and triple fusion have been observed.

Endosperm — The first division of the primary endosperm nucleus is followed by a transverse wall which results in the formation of a chalazal and a micropylar chamber (Figs. 55, 56). The former does not divide any further, and functions as an aggressive endosperm haustorium with a hypertrophied nucleus.

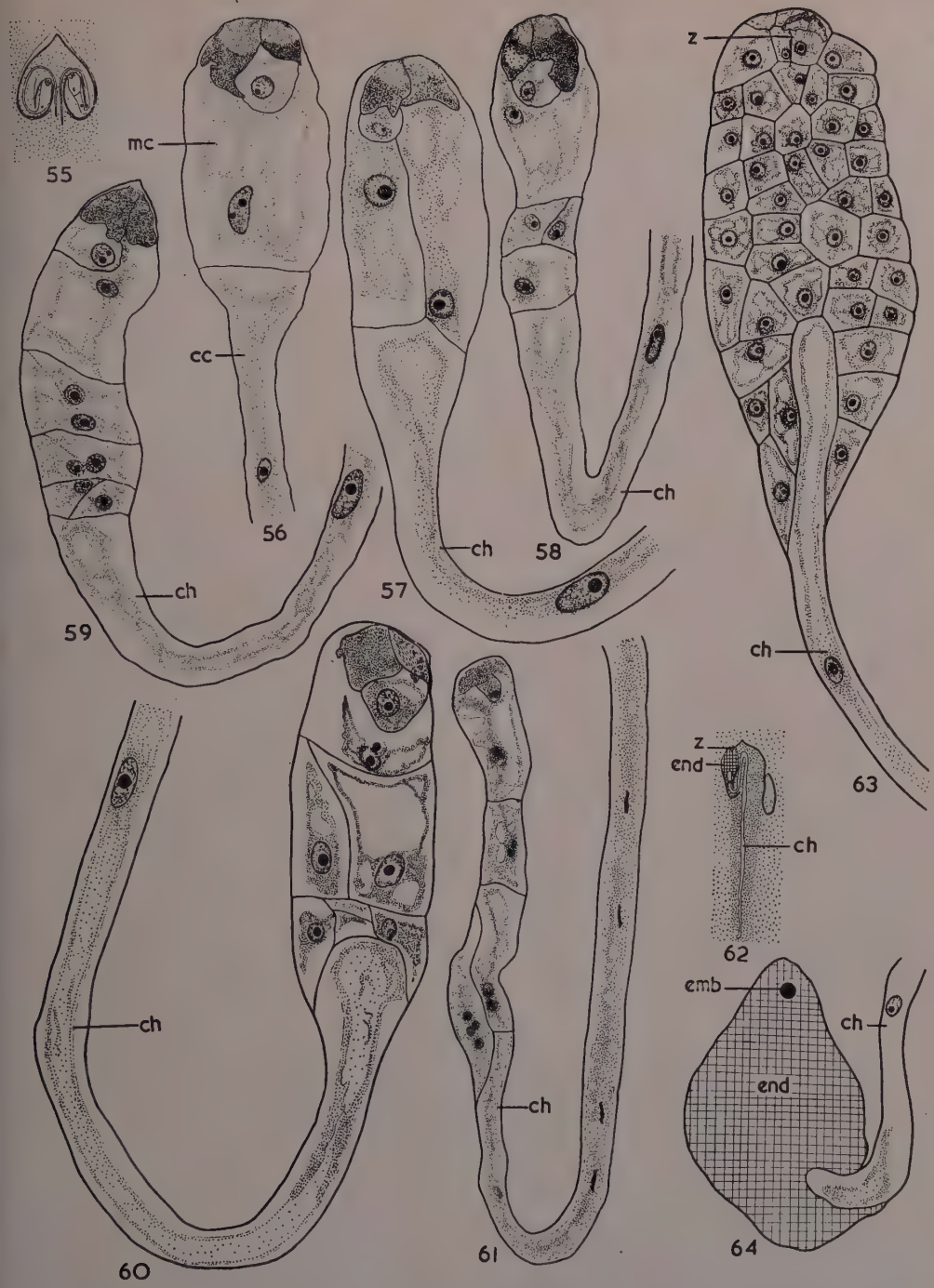
The first division in the micropylar chamber is usually transverse (Fig. 58) but sometimes it may divide by a vertical wall (Fig. 57). Later divisions are irregular and a mass of endosperm cells is produced (Figs. 59, 60, 62-64).

←

Figs. 21-44 — Microsporangium, microsporogenesis and male gametophyte (*dp*, degenerated pollen). Fig. 21. T.s. anther at microspore tetrad stage. × 117. Figs. 22-25. Parts of anther lobes at microspore mother cell, tetrad, uninucleate and 2-celled stage of pollen grains. × 480. Fig. 26. Microspore mother cell. × 960. Figs. 27-33. Meiosis I and II. × 960. Fig. 34. Cytokinesis. × 960. Figs. 35, 36. Decussate and tetrahedral tetrads. × 960. Fig. 37. ' Pentad '. × 960. Figs. 38-41. One and 2-celled pollen grains. × 480. Fig. 42. Acetolysed pollen grain. × 480. Fig. 43. T.s. dehisced anther. × 117. Fig. 44. L.s. anther (female flower) showing degenerated pollen grains. × 117.



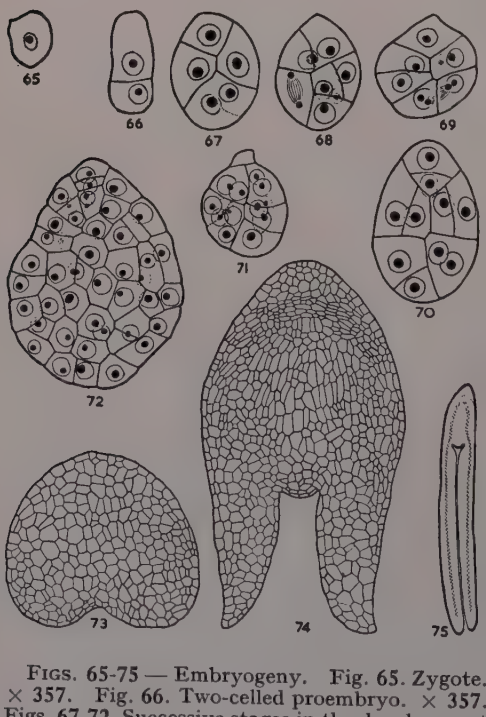
FIGS. 45-54 — Megasporogenesis and female gametophyte (*c*, chalazal caecum; *sn*, secondary nucleus). Fig. 45. L.s. ovule with three sporogenous cells. × 600. Figs. 46-48. Megaspore mother cell, tetrad and 2-nucleate embryo sac. × 600. Figs. 49, 50. Four-nucleate and organized embryo sacs. × 600. Fig. 51. Mature embryo sac; note the degenerated antipodal cells and chalazal caecum. × 600. Fig. 52. L.s. placental column showing disposition of embryo sacs (diagrammatic). × 64. Fig. 53. Embryo sac with the egg apparatus, secondary nucleus and chalazal caecum. × 345. Fig. 54. Zygote. × 600.



FIGS. 55-64 — Endosperm (*mc*, micropylar chamber; *cc*, chalazal haustorium; *emb*, embryo; *end*, endosperm; *z*, zygote). Fig. 55. L.s. placental column with two embryo sacs. × 28. Fig. 56. Enlargement of right embryo sac from Fig. 55 showing zygote and 2-celled endosperm, the chalazal chamber (haustorium) contains only a single nucleus in Figs. 57-60, 63, 64. × 264. Figs. 57-60. Progressive stages of endosperm development. × 264. Fig. 61. Abnormal endosperm with three uniseriate, binucleate cells; the chalazal haustorium shows one healthy nucleus and four degenerated masses; an arrested 4-nucleate gametophyte (?) is also attached to the endosperm. × 228. Fig. 62. Outline diagram for Fig. 63. showing placental column with embryo sac. × 15. Fig. 63. Multicellular endosperm, note the extension of the endosperm around the upper part of the chalazal haustorium. × 152. Fig. 64. Later stage in the development of the endosperm. × 40.

Fertilization may occur in all the three embryo sacs in an ovary but the endosperm develops in only one of them. Rarely, the endosperm may start developing in two embryo sacs but finally only one reaches maturity. In one of the embryo sacs all the endosperm cells were binucleate and an arrested 4-nucleate embryo sac (?) was attached to it (Fig. 61).

EMBRYO — The zygote (Fig. 65) does not divide until the endosperm becomes quite massive. The first division is transverse (Fig. 66) and the terminal cell gives rise to the embryo proper while the basal cell forms the single-celled suspensor (cf. Rao, 1942) which is usually difficult to trace in older stages (Figs. 67-72). In the light of these observations Guignard's (1885) report that the embryo of *Osyris* lacks a suspensor seems to be incorrect. The globular, heart-shaped and dicotyledonous stages follow in the usual way (Figs. 72-75). Due to insect attack the endosperm and embryo are destroyed in a number of young fruits.



FIGS. 65-75 — Embryogeny. Fig. 65. Zygote. × 357. Fig. 66. Two-celled proembryo. × 357. Figs. 67-72. Successive stages in the development of embryo. × 357. Figs. 73-75. Heart-shaped, young and mature dicotyledonous embryos. Figs. 73. × 87; 74, × 60; 75, × 14.

FRUIT — At the mature embryo sac stage the ovary wall consists of nearly 35 to 50 layers of parenchymatous cells (Figs. 76, 77). Stomata are present on the outer epidermis. At a later stage the hypodermal layers below the inner epidermis undergo periclinal divisions and the pericarp becomes still more massive. When the embryo reaches nearly 32-celled stage, the pericarp is distinguishable into the epicarp of large tanniniferous cells, mesocarp of isodiametric cells and a broad endocarp of thin-walled cells. At the globular stage of the embryo the cells of the mesocarp become thick-walled (Figs. 78, 79) and in a mature seed they form the stony zone. The broad parenchymatous endocarp is consumed by the growing endosperm so that only its remnants are seen at maturity (Figs. 80, 81).

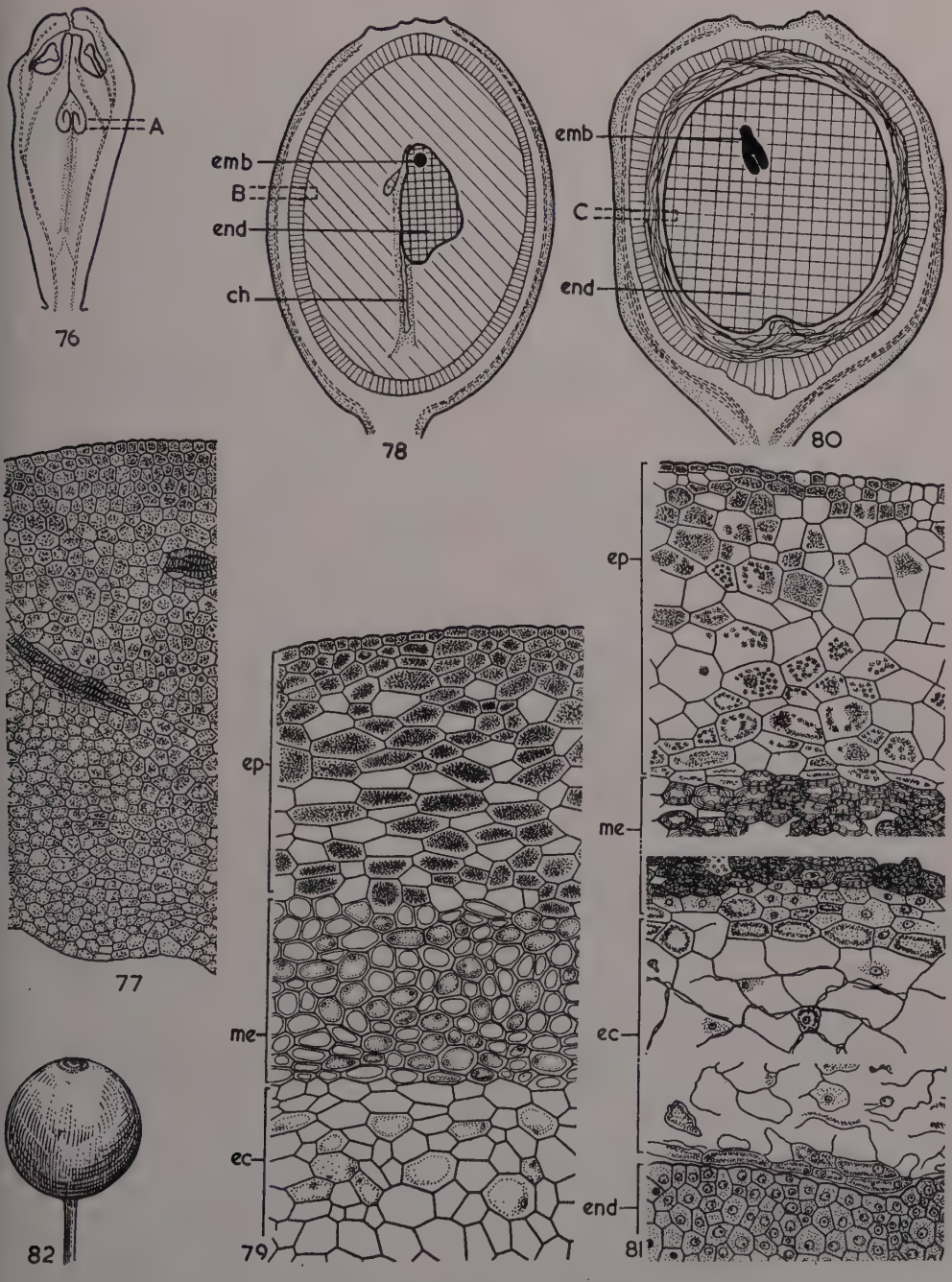
The fruit is a globose nut (Fig. 82) containing a single 'naked' seed in which the embryo occupies the apical region of the endosperm. The endosperm cells adjacent to the embryo are depleted of their contents and the outer tangential walls of the epidermis of endosperm develop a thin cuticle. The mature endosperm contains starch and some shining crystals.

Summary

The flowers are dioecious. The perianth is usually trimerous and the stamens are epiphyllous. In male flowers unicellular glandular hairs are present behind the stamens. The inferior ovary is trilocular below and unilocular above. The free central placenta is straight and dome-shaped and bears three anatropous ovules at the tip.

The anther wall comprises the epidermis, fibrous endothecium, single middle layer and glandular tapetum which remains uninucleate throughout. At maturity the adjacent pollen sacs become confluent and dehiscence occurs by two longitudinal slits.

The microspore mother cells undergo simultaneous reduction divisions and cytokinesis takes place by furrowing



FIGS. 76-82 — Pericarp (*ch*, chalazal haustorium; *ec*, endocarp; *emb*, embryo; *end*, endosperm; *ep*, epicarp; *me*, mesocarp). Fig. 76. L.s. flower at mature embryo sac stage. × 7. Fig. 77. Enlargement of portion marked A in Fig. 76. × 27. Figs. 78, 80. Longisections of fruits at globular and dicotyledonous stages of embryo. × 6. Figs. 79, 81. Enlargements of portions marked B and C in Figs. 78 and 80. × 107. Fig. 82. Mature fruit. × 2.

resulting in tetrahedral and decussate tetrads. The mature pollen grain is ovoid with three germ pores and is shed at the 2-celled stage.

The ovule does not show any distinction between nucellus and integument and there is no micropyle. Three or four hypodermal archesporial cells differentiate in the beginning but usually only one functions. The development of the embryo sac is of the Polygonum type and the chalazal end extends into a caecum leaving the antipodal cells *in situ*. The caecum invades the funiculus and the placental column. The mature embryo sac is ⌐- or ⌙-shaped and becomes exposed due to the absorption of the ovular epidermis.

The endosperm is Cellular. The first division of the primary endosperm nucleus results in a micropylar and a chalazal chamber. The endosperm proper is produced by the former while the chalazal chamber functions as a uninucleate haustorium.

The first division of the zygote is transverse and the mature embryo has the usual two cotyledons. The endosperm consumes the ovular tissue, placental column and parenchymatous endocarp so that in the mature fruit it is surrounded by the remnants of the endocarp followed by stony mesocarp and parenchymatous epicarp.

I take this opportunity to express my gratitude to Dr B. M. Johri and Professor P. Maheshwari for giving me the facilities and encouragement for carrying out this investigation.

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OBSERVATIONS ON TRACHEARY ELEMENTS

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Introduction

Systematic studies of the secondary xylem of Angiosperms (*see* Tippo, 1946; Metcalfe & Chalk, 1950) have proved themselves to be extremely valuable in our understanding of the various cell types and cell arrangements from a phylogenetic point of view and have assisted greatly in adding more naturalness to current systems of classification. The efficient pursuit of these studies and also the effective use of the results were dependent on a complete, unambiguous, widely accepted, and objective system of descriptive terms. Studies of the tracheary elements of the early formed xylem have not yet reached this advanced stage, despite the fact that the literature on the subject is voluminous. Terminology has not been standardized, but often differs from author to author. Wherever terms such as "scalariform", "reticulate", and even "helical", "annular", and "pitted" are used without accurate descriptions and illustrations the meaning of the author is in doubt. Where the applications are made clear by appropriate illustrations, it is often found that the usages are highly variable. These generalities are made clear in the tables presented in the discussion at the end of this paper. Many citations were necessarily omitted from these tables because it was not possible to determine precise usages. In actuality, a large part of the material present in the literature in which tracheary elements are described is essentially lost to us through ambiguity.

The need for a relatively complete system of classification of the various types of tracheary elements is brought out by the great range in variability presented in the descriptive portions of this paper. Much of this variability would be obscure and relatively unusable if currently available, vague and all-inclusive terms were used to describe them. It is suggested from the present study and others mentioned below that there are several relatively distinct types of "reticulate" elements among the Angiosperms some of which may be restricted to certain families or groups of closely related families. The extent to which this statement is accurate is obviously dependent on future angiosperm survey type studies. Without proper specific terminology the distinctiveness of these "reticulate" elements is lost and hence the information is not usable. The recognition of certain types of simple reticulate and modified annular types adds significantly to an ultimate understanding of the relationships among some of the lower vascular plants. By proper description and terminology it is brought out that the Lycopodiaceae is probably very remote from the Selaginellaceae. Complete descriptions of early protoxylem elements of the ferns support previous suggestions that the Ophioglossaceae is relatively close to the Marattiaceae and that the Osmundaceae is closer to the above mentioned families than are any of the higher Filicalean families.

When walls are referred to as being lignified or unlignified the information is derived for the most part from sections stained with haematoxylin, safranin, and fast green or safranin and fast green only. The phloroglucinol-HCl reaction was used on several occasions on similar sections and was found to give the same results. Scarth *et al.* (1929) found correspondence between the phloroglucinol reaction and reactions with basic stains. Harlow (1928) indicates that deductions based on the phloroglucinol reaction must be taken with

reservation following the report of Crocker (1921) that phloroglucinol indicates only a particular portion of the lignin. Preston (1952) indicates that the phloroglucinol test is not specific for lignin. With the above indicated potential error in mind, the observations are presented. It is not the intent in this paper to characterize the primary xylem elements of all of the various plant groups included in this study. This is only too obvious from the very disproportionate sampling. The ultimate aim is a generalized concept of cell wall patterns and an interpretation of the more elaborate types of elements as well as the development of a usable system of classification of the various types of tracheary elements.

Materials and Methods

Sources of materials varied widely. Collections of both native and cultivated forms were made during the period from 1946 to 1959 in the vicinities of New Orleans, La., Minneapolis, Minn.; and Ithaca, N.Y. Living materials, especially ferns, were available in variety from the collections of the L.H. Bailey Hortorium and the Department of Botany at Cornell University and also the Department of Botany of the University of Minnesota. Preserved materials collected by J. Tilden in the Islands of the Pacific were available at the University of Minnesota as well as from the collection assembled by Professor A. J. Eames at Cornell University.

The following is a list of the species included in the study:

Psilotum nudum
P. complanatum
Tmesipteris tannensis
Lycopodium selago
L. obscurum
L. clavatum
L. lucidulum
L. complanatum
L. phyllanthum
L. cernuum
L. volubile
Phylloglossum dramondii
Isoetes engelmani
I. muricata
Botrychium virginianum
B. multifidum
B. dissectum
B. simplex
Ophioglossum vulgatum
O. pendulum
Helminthostachys zeylanica
Angiopteris evecta
Marattia alata
Danaea sp.
Osmunda cinnamomea
O. regalis
Todea hymenophylloides
Schizaea pusila
Anemia phyllitidris
Trichonomes sp.
Dicksonia sp.
Cibotium sp.
Dennstaedtia sp.
Pteridium aquilinum
Coniogramme japonica
Pellaea rotundifolia
Adiantum pedatum
Davalia fejiensis
Humata tyermanni
Nephrolepis exaltata
Pteretis nodulosa
Onoclea sensibilis
Dryopteris marginalis
Cystopteris fragilis
Blechnum sp.
Doodia maxima
Asplenium bulbiferum
A. trichonomes
A. viride
Scholopendrium sp.
Polypodium peroussum
Marsilea quadrifolia
Salvinia sp.
Cycas revoluta
Ceratozamia sp.
Dioon spinulosum
Ginkgo biloba
Taxus baccata (*sens. lat.*)
Cephalotaxus sp.
Araucaria excelsa
Taxodium distichum
Podocarpus macrophylla
Pinus mugho
P. banksiana
P. sylvestris
Picea abies
Tsuga canadensis
Larix laracina
Cedrus deodara
Cupressus sempervirens
Junipersus virginiana
Ephedra foliata
E. antisiphalitica
E. sp.
Welwitschia mirabilis
Gnetum leyboldii
G. schwackeanum
G. venosum
G. gnemon
Liriodendron tulipifera
Magnolia grandiflora
Michelia fuscata
Casuarina equisetifolia
Ligustrum vulgare
Hedera helix
Hibiscus esculentus
Citrullus vulgaris
Dracaena fragrans
Cordyline sp.
Aloe arborescens

Standard techniques of fixation, dehydration, embedding and staining were used. The most satisfactory staining procedure followed was one in which a combination of Heidenhain's haematoxylin, safranin, and fast green was employed.

A Note on Terminology

Early formed primary tracheary elements are often seen to have a relatively thin, continuous, unlignified first-formed wall and a relatively thick, discontinuous, lignified later-formed wall. Such a cell often enlarges or is stretched after com-

pletion of differentiation and maturation. During the stretching process, the first-formed wall is stretched. To this cell one can apply the terms primary wall (first-formed wall) and secondary wall (later-formed wall) with clarity and without ambiguity. The definition recommended by Bailey (1957) and more or less followed by Esau (1953) and by Eames & McDaniels (1947) in terms of stretchability is completely satisfied, as well as that apparently adhered to by Barghorn & Scott (1958) in terms of lignification. Similarly, the concept of Frey-Wyssling (1948, 1950) and Mühlenthaler (1950) of the primary wall as a very thin layer of cell wall deposited first is satisfied. And furthermore, the first-formed wall of the above described cell is comparable in many ways, although possibly not as thin, to the primary wall described by Preston (1952) in the wall of a tracheid from the secondary xylem of *Pinus*.

Among the extant vascular plants, the range in variation of early-formed primary xylem elements includes cells with:

(a) A thin, unlignified, continuous first-formed wall and a thicker, discontinuous, lignified later-formed wall;

(b) As in a, but portions of the later-formed wall are deposited on the first-formed wall at various times in the ontogeny of the cell; in addition, the later-formed portions of the later-formed wall may be either in strands or in sheets and may be deposited only onto the first-formed wall (and form pits!) or onto both the first-formed wall and the first-formed portions of the later-formed wall;

(c) As in a or b but first-formed wall is relatively thick and either lignified (after stretching) or unlignified, also it may become thick before elongation has ceased;

(d) As in a, b, or c, but later-formed wall showing various degrees and patterns of lignification, e.g. outer part of discontinuous wall unlignified (either continuously or discontinuously) and inner part lignified; or inner and outer part of discontinuous wall unlignified and middle part lignified; or patterns of lignification varying over different areas of cell;

(e) A thin, unlignified, continuous first-formed wall and a thicker continuous (except at pits) later-formed wall;

(f) As in e, but only the first-formed part of the later-formed wall is continuous, the inner part of the later-formed being discontinuous;

(g) As in e or f except lignification complete throughout wall (after stretching process is completed) or showing various degrees and patterns of lignification.

It seems clear that a working concept[1] of the primary and the secondary wall must be completely divorced from any consideration of lignification. It might be said that secondary walls are more often lignified than primary walls and that lignified walls are slightly if at all stretchable. But, nevertheless, lignification, it seems, must be regarded as an incidental secondary modification or else the entire usefulness of the concept of the primary and the secondary walls will be destroyed.

The usefulness of the terms is similarly imperiled if thickness or thinness is emphasized. Esau (1953) states that the primary wall may be very thin or relatively thick and multi-layered; whereas Frey-Wyssling (1948, 1950) and Mühlenthaler (1950) might restrict it to a very thin membrane. We are, to be sure, most familiar with the detailed structure of the very thin type of primary wall from recent studies with the electron microscope and less recent with polarized light; but this is no reason why this type of primary wall should dominate our concept. This would parallel the situation where the morphology of the Coniferales is described and thought of in terms of the Pinaceae (*sens. strict.*) or where the morphology of the ferns is described and thought of in terms of the higher leptosporangiate ferns, merely because certain genera are well known and occur in temperate regions in the vicinity of the larger universities[2].

The usefulness of the concept of the primary wall depends on its definition in terms of stretchability and correlated

1. It is not the intent in this discussion to resolve or attempt to resolve the question as to whether or not there is a real and natural and consistent difference between the primary and the secondary wall, but to merely arrive at a workable concept. The terms in question have proven very useful in the past and it is quite improbable that they will be dropped from botanical usage in the foreseeable future.

2. This has been done!

submicroscopic structure, previous to secondary modifications such as lignification. If stretchability cannot be determined, the wall in question should be referred to as a presumed primary wall rather than a primary wall.

Descriptions of Some Tracheary Elements

LYCOPODIACEAE—*Lycopodium*: The first protoxylem elements to mature in the stem, root and leaf of *Lycopodium* are of a modified annular type. They are characteristic of the genus and are probably of diagnostic value. They are narrow, long elements occurring in groups of up to 20 or more cells (as seen in cross-section) with few or no intermixed parenchyma cells. The latter feature could probably be used to separate *Lycopodium* from all other extant vascular plants. The elements possess a delicate, unlignified primary wall with a series of annular thickenings on the inside. Adjacent rings are in turn interconnected by one or two vertically or obliquely oriented thickenings (Figs. 1-3). The interconnecting thickenings usually do not suggest helical bands between rings as are found in other groups such as angiosperms. Occasional rings are free from adjacent ones. In later formed elements of this type, the interconnections between adjacent rings are broader and more nearly vertically oriented (Fig. 4). The breadth of the interconnection may be so great that it appears as a sheet covering up to one-fifth of the surface area between adjacent rings. It is suggested that this type of element be called an *indirectly attached annular element*. This term would include elements found in the Lycopodiaceae, Equisetaceae, Marattiaceae, and Ophioglossaceae, each, however, with its own individuality.

The later formed protoxylem elements of *Lycopodium* possess a delicate, unlignified primary wall internal to which is a discontinuous system of thickenings in the form of a net (Figs. 6, 7). When this type of element is unstretched (Fig. 8), it might easily be confused with a helical element. The term *simple reticulate element* seems ideally appropriate in this instance. The forks and anastomoses (and consequently openings) in the early *reticulate elements* of *Lycopodium* are situated with only partial regard for cell faces and cell edges. The centres of the openings tend to be situated near the centres of the faces and therefore the forks and anastomoses tend to be in the vicinity of the cell edges. This is true even though the openings in the reticulum are broader than the faces and therefore overlap the edges.

There are elements which are somewhat intermediate in form between the *indirectly attached annular elements* and the *reticulate elements* (Fig. 5). There are no helical elements in *Lycopodium*.

In the transition from protoxylem to metaxylem in *Lycopodium* the discontinuous wall of the *reticulate elements* gradually assumes a more extensive nature (Figs. 9-11) with smaller openings which themselves gradually assume more extensive borders. The border, i.e. the overaching of the continuous wall by the discontinuous wall, is actually present to a degree in all of the tracheary elements of *Lycopodium* (Fig. 21). The openings, as well, become more and more restricted to cell faces, until toward the end of the transition, none of the openings intersect or cross cell edges and they are all essentially in uniseriate order on a given face and alternate with those on adjacent faces. At the end of the transition one finds openings in the inner wall which satisfy all criteria for bordered pits.

The pits are circular bordered in the narrower elements (Figs. 12-14) and elongate in the broader elements (Fig. 15). The elements with transversely elongate or scalariform pits follow ontogenetically those with circular bordered pits. Often scalariform pitting is absent, e.g. most stems of *L. selago*. Elements with circular bordered pits are regarded here as being at the same stage of phylogenetic specialization as those with scalariform pitting within the genus *Lycopodium*.

Lignification in the protoxylem and early metaxylem of *Lycopodium* is very sparse. The thickenings of the discontinuous wall possess an extensive unlignified (or very faintly lignified) core (Fig. 21, blackened area) with a relatively thin lignified covering. How much of the

discontinuous wall is truly secondary in the sense proposed by Bailey (1957) is difficult to determine, but this question will again arise below.

Phylloglossum — In conformance with the interpretation that *Phylloglossum* is a reduced form, the xylem elements of this genus are all of a relatively simple annular type (Figs. 16, 20). The elements possess a thin, unlignified primary wall internal to which are a series of thickenings in the form of rings which are usually lignified. The rings may occasionally fork (Figs. 16, 20, right side) or adjacent rings may occasionally be attached directly (Fig. 20, left).

Directly attached annular element is proposed as a descriptive term for elements with a series of rings which are attached to each other directly, not by means of interconnecting strands. This type of element has been found in *Equisetum* (Bierhorst, 1958), but here in *Phylloglossum* direct attachment is only occasional between pairs of adjacent rings. The term *simple annular element* is proposed for elements with a series of discrete rings without other elaborations.

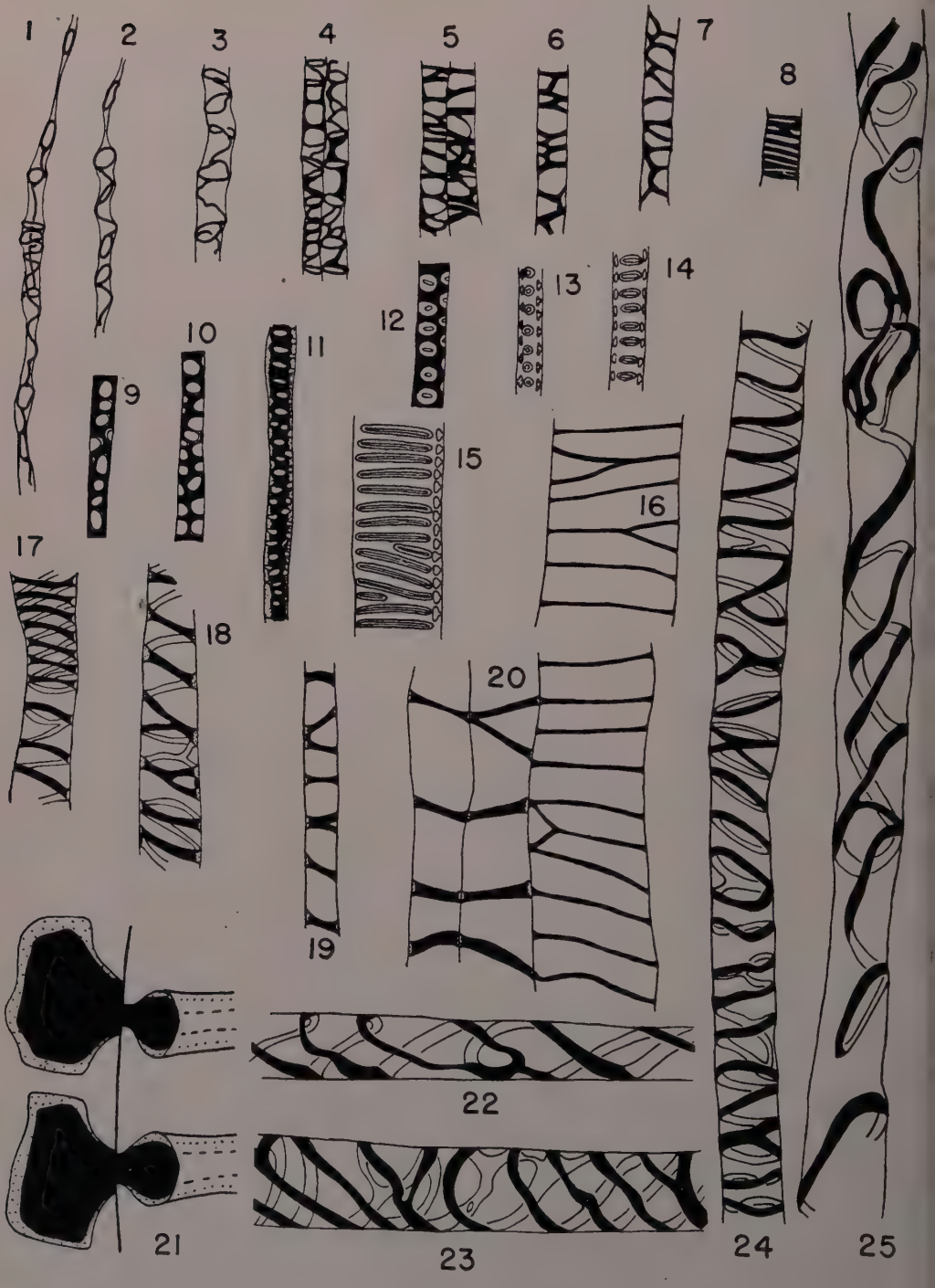
SELAGINELLACEAE—*See* Zamora (1958).

ISOETACEAE — Aside from the queer, isodiametric elements found in the "secondary" xylem of the corm of *Isoetes*, the xylem is entirely protoxylem and composed of annular and helical elements with some peculiarities. The annular elements possess a thin, unlignified primary wall and a series of lignified (often weakly) rings which may be forked or directly attached (Fig. 19) as in *Phylloglossum*. The later formed elements similarly have a thin unlignified primary wall and a lignified discontinuous wall. The discontinuous wall is often in the form of a simple, single helix (Fig. 18, upper part) through a large part of the cell or occasionally a pair of simple helices is present (Fig. 17, upper part). The helix or helices are rarely if ever continuous throughout a given cell, but end with a ring (Figs. 17, 18) with a new helix continuing from another ring. The double helix seems generally to end with a complete ring and not by a simple connection between the two (Fig. 169, bottom) or by blind endings of each of the two helices. The helical thickenings may be wound in different directions in different parts of the same cell in *Isoetes*, a feature known to occur elsewhere only in *Selaginella* (Zamora, 1958). Occasional forks and anastomoses occur in the helical elements of *Isoetes* (Fig. 18).

For convenience of description the following terms are proposed to describe helical elements. The term *simple helical* is proposed to describe elements which possess simple, unelaborated spiral thickenings. In addition the adjectives *single*, *double*, or *multiple* are added to complete the description of elements with one, two, or more individual spiral bands running parallel and independent of each other. The term *reversed helical* is proposed to describe elements in which the spirals are wound in different directions in different parts of the same cell.

Previous descriptions of tracheary elements of the lycopods are for the most part meager and uninforming, at least in the context of the present study, which for the most part concerns itself with highly specific characteristics of the type which were not of prime interest to previous workers. This, coupled with the facts that (1) descriptions of most primary tracheary elements have been presented as quite incidental observations to other anatomical studies; (2) descriptive terms for primary tracheary elements have been used in very ambiguous ways (*see* discussion) and without accurate illustrations it is often impossible to determine the way in which a given term is being used; and (3) interpretations of the overall patterns of thickening in tracheary elements are more often based on observations of one side of an element, e.g. unstretched simple reticulate elements are generally referred to as helical, makes it difficult to make full use of comments available in published literature.

The primary xylem elements of *Lycopodium* have been described as spiral followed by scalariform in the ontogenetic sequence (Campbell, 1928). Those of *Isoetes* as spiral or ring form (Ogura, 1938). The elements of several fossil forms have been described, e.g. LeClerc (1930) describes elements of *Stigmaria* as spiral and annular followed by barred



FIGS. 1-25.

elements, and Fry (1954) describes the elements of *Paurodendron* as annular, spiral and scalariform. The so-called Williamson's striations of the fossil lycopods will be discussed below (*see* discussion).

EQUISETACEAE — *See* Bierhorst (1958).

PSILOTACEAE — The first protoxylem elements to mature in the aerial stems (there is no protoxylem in subterranean stems) of the Psilotaceae are massive in size as compared to comparable elements of *Lycopodium*. This can be appreciated by comparing Figs. 22-27 with Figs. 1-7 all of which are reproduced at the same scale.

The early protoxylem elements of *Psilotum* and *Tmesipteris* are extremely similar if not essentially identical. They are similarly highly distinctive for the family. If, however, they are described as helical or annular-helical, their distinctiveness becomes lost. One can find in these elements (Figs. 22-26) some simple, unattached rings (Figs. 24, 26) as well as simple, unelaborated helical portions (Fig. 24, top, single helix; Fig. 25, centre, double helix). The helical portions terminate at a single ring (Figs. 24, 25), or with a dead end (Fig. 26, centre), or with a complex girdle (Fig. 26, top). Single helices often become double helices by a simple branching (Figs. 23, 25, 26). Annular thickenings may be directly attached to each other at an edge or they may be forked near their mid-sections (Fig. 24). Often small slit-like openings are found within a thickened band (Figs. 23, 26). These are not merely areas where the spiral thickening is slightly thinner than elsewhere, as in some other plant groups, but complete gaps in the thickening. The thickenings, both ring and helical, show a waviness or variation in width and seem not to fall along smooth curves, but to lay out a slightly sinuous path (Figs. 22-26).

In *Tmesipteris*, following ontogenetically the protoxylem elements are a series of distinctive reticulate elements (Figs. 35-37) with relatively large, often squarish, slightly bordered openings which are essentially all restricted to cell faces. In the progression of cell types (Figs. 35-39) the openings become less squarish, more spaced, more transversely elongate, and assume broader borders and narrower apertures, culminating in the later metaxylem with typical scalariform bordered pits (Fig. 39). This transition seems to be less gradual in *Psilotum* with reticulate-like elements less common. Elements similar to the one shown in Fig. 36 may, however, be found in *Psilotum* (*see* Fig. 9, in Moore & Andrews, 1936). Figures 32 and 33 represent portions of elements from the early metaxylem of *Psilotum*. Figure 34 shows a feature not uncommon in *Psilotum*, but extremely rare among non-seed bearing vascular plants. This is the presence of extensive areas of thick wall very sparsely pitted. In the figure, the three small pits on the right are on one cell face which abuts onto parenchyma, while the row of larger pits on the left are on another face which abuts onto another tracheid. In *Psilotum* the condition of sparse pitting is to be found only on walls common to tracheids and parenchyma.

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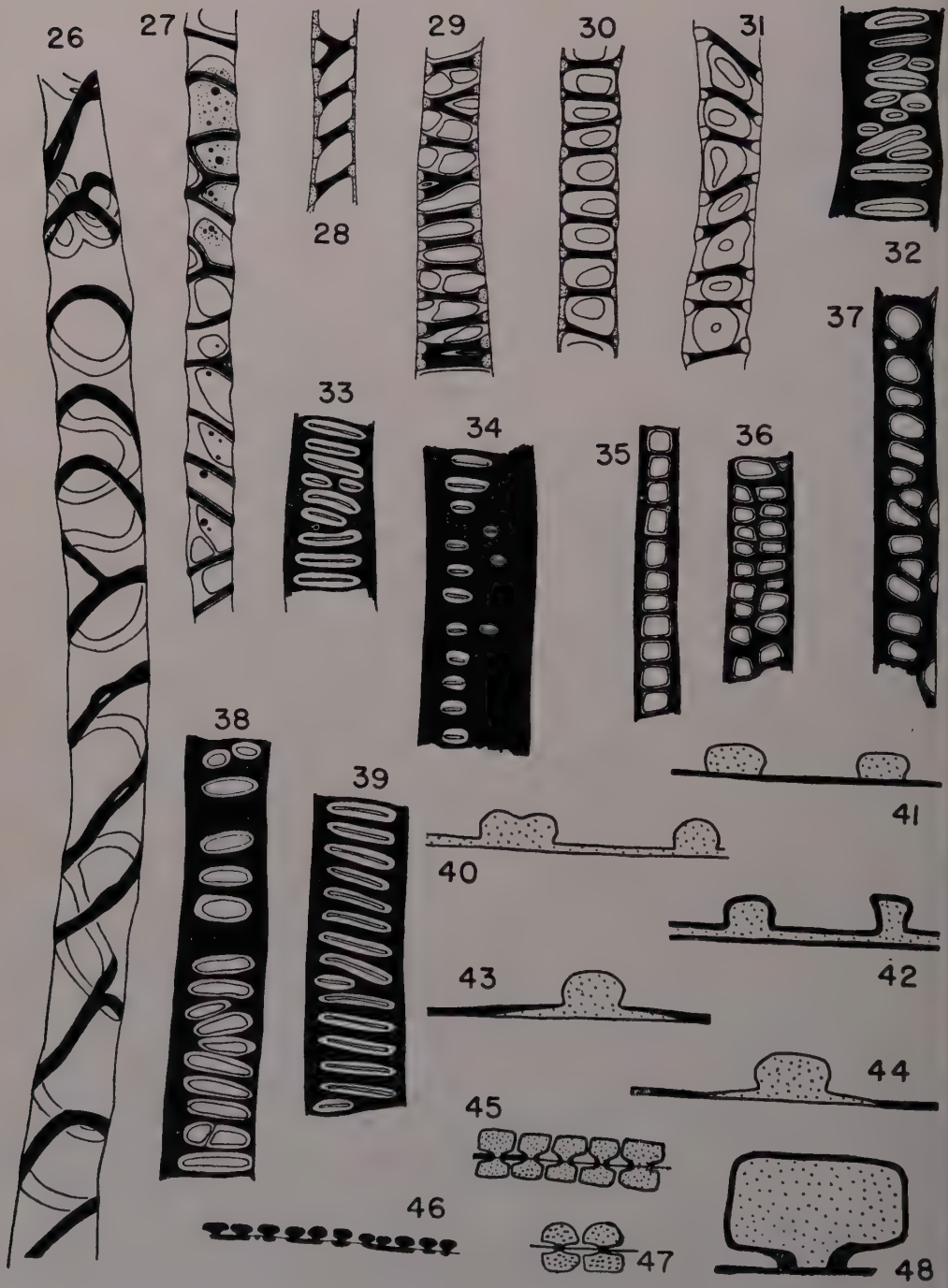
FIGS. 1-25 — Figs. 1-4. Portions of early protoxylem elements from the stem of *Lycopodium obscurum*. × 666. Fig. 5. Portions of two adjacent elements of the intermediate protoxylem from the stem of *L. obscurum*. × 666. Figs. 6, 7. Portions of stretched reticulate protoxylem elements from the stems of *L. selago* and *L. obscurum*, respectively. × 666. Fig. 8. Portions of an unstretched protoxylem reticulate element from the stem of *L. obscurum*. × 666. Figs. 9-11. Portions of reticulate elements of the early metaxylem of the stem of *L. selago*, *L. selago*, bordered to scalariform pitted elements from the stems of *L. selago*, *L. obscurum*, *L. obscruum* and *L. obscurum*, respectively. × 666. Figs. 16, 20. Portions of tracheary elements from a new tuber and from the strolibus of *Phylloglossum*, respectively. × 666. Figs. 17-19 Portions of tracheary elements from the leaf trace of *Isoetes engelmani*. Figs. 18, 19 from the trace deep in the tissues of the corm. × 666. Fig. 21. Portions of the walls of two adjacent tracheary elements of the stem of *Lycopodium obscurum*. Protoxylem element on the right, metaxylem element on the left. Black represents unlignified wall; stippling represents lignified wall. × 7300. Figs. 22-25. Protoxylem elements from the aerial stem of *Psilotum nudum*. × 666.



FIGS. 26-48.

The pitting in the late metaxylem elements of the *Psilotaceae* can be described as uniseriate (Fig. 34), alternate or irregular (Fig. 32) on a given face and alternate across the cell edges from face to face. In shape the pits vary from circular bordered (Figs. 32, 38) to scalariform bordered. Elongate pits in a given element may be matched occasionally with horizontal pairs of pits in adjacent elements. In face view, such pit systems give the impression of elongate pits partly separated into smaller pits. It is difficult to determine from the illustrations of Moore & Andrews (1936, Figs. 6, 9) whether the apparently "dividing pits" are in reality what they are presented to be or merely face views of pit systems in which a single pit is matched with a pair of pits.

The application of the expression "transitional pitting" (Moore & Andrews, 1936) to the Psilotaceae will be discussed in a more general context.

The early protoxylem elements of both *Psilotum* and *Tmesipteris* first develop a thin, elastic primary wall then the characteristic lignified secondary thickenings. They may then loose their protoplasts and cease to change, save for being stretched passively. On the other hand, many, if not most, of the protoxylem elements produce more cell wall after the typical secondary thickenings are completely formed. This additional wall is deposited over the primary wall and either covers all or part of the area between the secondary thickenings. Figure 28 illustrates a portion of a protoxylem tracheid of *Psilotum* with the additional wall (shown in sectional view) covering the primary wall. In this instance the additional wall was complete and uninterrupted except at the secondary thickenings. For purposes of description and discussion it is essential that terminology be proposed for the additional wall. The term "tertiary wall" is obviously inappropriate because of its application in a different sense. The expression *secondary secondary wall*, although possibly a bit clumsy, seems appropriate.

The *secondary secondary wall* may be deposited as a sheet extending only a short distance outward from the thickenings of the secondary wall (Fig. 27), or it may be more extensive outlining simple pit-like areas between the secondary thickenings (Fig. 27, in part; Figs. 29, 30, 286). When these pit-like areas are well defined they tend to be restricted to cell faces and tend to avoid crossing cell edges. The pit-like areas are often squarish in outline and when restricted to cell faces give to the cell the aspect of the curious reticulate-like elements described above. Occasionally the secondary secondary wall is in the form of discs with a central aperture (Fig. 31), superficially resembling a series of bordered pits between the ordinary secondary thickenings.

Patterns of lignification in the tracheidal walls of the Psilotaceae are quite variable. These are shown in Figs. 40-45, 47, 48 where lignified wall is stippled and unlignified wall is blackened. In Fig. 40, a portion of the wall of the element shown in Fig. 26 is shown; here the entire wall is completely lignified. Figures 43 and 44 show other portions of the wall of the same tracheid of Fig. 26, where the helical thickening is lignified as well as the wall toward the outside and the wall adjacent to the thickening and extending outward from it. Figures 41 and 42 show portions of opposite sides of another protoxylem element where (Fig. 41, which is the side

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FIGS. 26-48 — Fig. 26. A portion of a protoxylem element from the aerial stem of *Psilotum nudum*. × 666. Figs. 27-31. Portions of protoxylem elements from the aerial stem of *P. nudum* showing the secondary-secondary wall. Structures in Figs. 30 and 31 are not bordered pits; *see* text. × 666. Figs. 32-34. Portions of metaxylem elements from the aerial stem of *P. nudum*. × 666. Figs. 35-39. Same from *Tmesipteris tannensis*. × 666. Figs. 40-45, 47, 48. Sectional views of portions of walls of tracheary elements of *Psilotum nudum*, showing patterns of lignification. Black represents unlignified wall; stippling represents lignified wall. Figs. 40, 43, and 44 are taken from various parts of the cell shown in Fig. 26. Figs. 41 and 42 are taken from opposite sides of the same cell. Figs. 40-44. × 2660. Figs. 45, 47. × 1330. Figs. 48. × 7990. Fig. 46. Sectional view of the wall of a metaxylem tracheid and adjacent parenchyma cell from the stem of *Tmesipteris tannensis*. × 666.

of the element bordering on parenchyma) the continuous wall is unlignified and the discontinuous wall is lignified and where (Fig. 42, which is the side of the element bordering on another tracheid) there is an outer and an inner layer of unlignified wall and a middle zone of lignified wall. Later formed metaxylem elements show a thin, unlignified primary wall on which the pitted wall is inserted. The thickening of the pitted wall, i.e. the portions between the circular bordered to scalariform bordered pits, may be entirely lignified except for a small ridge connecting them to the primary wall (Fig. 47) (*see* Esau, 1953, p. 229). The primary nature of this ridge will be discussed in connection with certain ferns below. There may be an unlignified zone on either side of the connection (as seen in sectional view), actually completely encircling the pit chamber (Figs. 45, 48). This is usually responsible for the sharpness with which the pit borders are seen in face view and may, in addition, give a false impression of a thickened pit-closing membrane if the focal plane is not carefully controlled (Fig. 45, left side). The unlignified areas bordering the pit chambers tend to thin out gradually from the primary wall inward and may even extend entirely over the wall surface (Fig. 48).

Pit matching between metaxylem tracheary elements and parenchyma often tends to be irregular in the Psilotaceae. This is shown in Fig. 46.

The tracheary elements of the Psilotaceae have been described as spiral in the protoxylem and scalariform in the metaxylem (Eames, 1936; Campbell, 1928; Ford, 1904). Annular thickenings were mentioned by Moore & Andrews (1936) and Ogura (1938).

MARATTIACEAE — The tracheary elements of the Marattiaceae show a number of peculiarities; none, however, are unique to the family. The earliest protoxylem elements (Fig. 49) have thin, unlignified primary walls and a secondary wall in the form of a system of rings interconnected by finer strands which are vertically or obliquely oriented. The interconnecting system between the adjacent rings in progressively later formed elements tends to become more extensive and here and there forms a limited reticulum (Fig. 50). The element shown in Fig. 49 is classified as a form of *indirectly attached annular element*. The term *annular-reticulate element* is proposed to cover elements in which adjacent rings are interconnected by a network of strands. This is not to be confused with the *reticulated annular element* in which the rings are distinct and unattached, but each one is in the form of a reticulum as occurs in *Equisetum* (Bierhorst, 1958). The more simple *indirectly attached annular element* shown in Fig. 49 was observed only in *Marattia* in the Marattiaceae; however, elements extremely similar to the element shown in Fig. 50 were seen in each of the three Marattiaceous genera studied. Portions of the *indirectly attached annular elements* and the *annular reticulate elements* suggest portions of helices, more so in *Angiopteris* than in either *Marattia* or *Danaea*. In the later formed protoxylem elements (Figs. 51, 52) strands of the reticula between adjacent major thickenings of the cells become progressively thicker until they are of the same magnitude as the major thickenings themselves. At this point the distinction between the two systems of thickening is lost and the cell must be described as a *reticulate element*. This transition appears more extensive in *Marattia* and in *Danaea* than in *Angiopteris*. In the later formed protoxylem *reticulate elements* of *Marattia*, in addition to the more typical meshes in the network, there are rarely present circular, distinctly bordered pits (Fig. 52).

The transition from protoxylem to metaxylem involves a shift in the relative positions of the forks and the anastomoses of the secondary network so that they tend to be associated with cell edges. The transition is not abrupt, but gradual, so that at first the openings in the network show a partial regard for cell faces and cell edges and later they are more or less entirely restricted to cell faces and do not cross cell edges. In a given portion of an element the openings may be entirely restricted to cell faces, while elsewhere on the same cell openings may cross cell edges. Figure 53 shows a portion of an element where the openings are restricted to cell faces; a cell edge is present running vertically down the centre of this part of the

cell. On the portion of the element shown in Fig. 54 the central row of openings and the two rows partially shown are essentially restricted each to a given face, but as can be seen, this is not as complete restriction as is shown in Fig. 55. Figure 60, on the other hand, shows what is merely a tendency toward restriction of openings to cell faces.

In the transition within the early metaxylem, the reticulate openings develop progressively broader borders and assume the form of typical scalariform bordered pits (Fig. 64). In *Angiopteris* even at this point in the succession one can occasionally observe incomplete restriction of openings to cell faces (Fig. 61).

In the tracheary elements of the Marattiaceae, as in several other groups, there is a small ridge of unlignified wall material between the typical thin primary wall and the secondary thickening (Figs. 58, 62). That this ridge is primary wall and can be referred to as the *primary ridge* seems fairly certain for the Marattiaceae, Osmundaceae, and certain angiosperms. In *Berberis* (Abbot, 1959) the ridge is formed before the tracheary element reaches maximum diameter; in other words, it is stretched laterally.

In *Angiopteris* (Fig. 56), at the points of branching within the reticulum of the early to late protoxylem, there is no direct or abrupt connection, but there is an extended groove beyond the point where two converging strands first touch each other (Fig. 57). The *primary ridge* is relatively pronounced in these elements (Fig. 58) and extends along the groove to a point beyond where the secondary thickenings separate (Fig. 58). When these elements are stretched there may be a sharp bend produced at the point of connection (Fig. 59) and/or the two converging strands may separate along the groove and thus stretch the *primary ridge* in a vertical direction.

That the primary ridge can be referred to as the morphological equivalent of the "Rim" or "Bar" of Sanio seems relatively clear from the work of Bailey (1919).

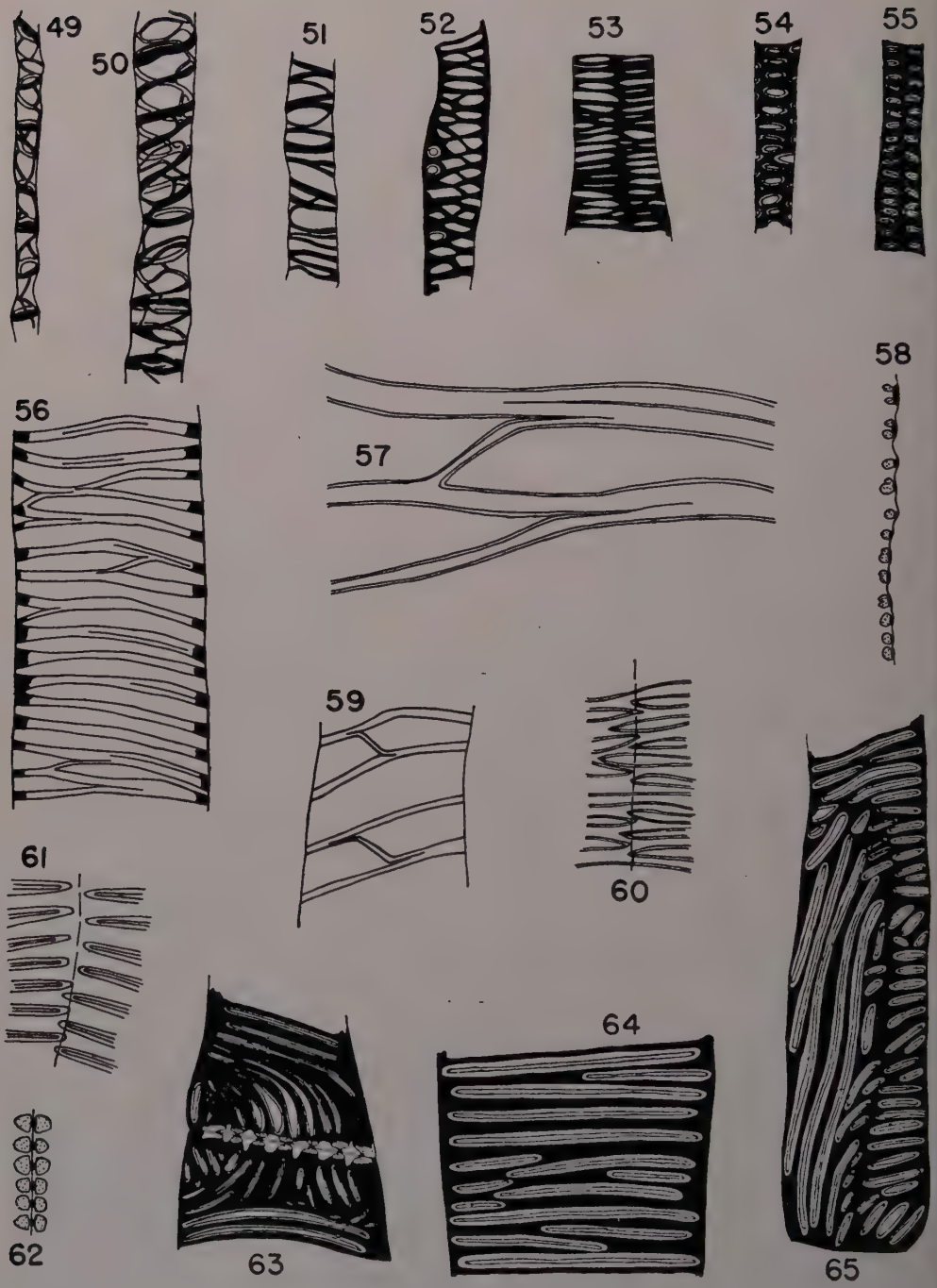
The scalariform bordered pits in the later metaxylem of the Marattiaceae alternate across the cell edges (Fig. 61). This is not surprising if essentially each one represents a single modified opening in a reticulum and their restriction to cell faces followed a sequence illustrated by Figs. 52, 60, 61. The term *trans-edge alternate pitting* is proposed to describe the pit arrangement described above and which similarly occurs in the scalariform elements of the Lycopodiaceae, Selaginellaceae, Psilotaceae, Cyacadaceae, and to some extent in the Osmundaceae. *Trans-edge opposite pitting*, on the other hand, is almost general among the higher leptosporangiate ferns and angiosperms.

Scalariform elements in which many of the elongate pits are oriented in a near vertical or lengthwise direction (Figs. 63, 65) have been observed in *Angiopteris*. This is generally associated with pitting in the opposing wall of the adjacent cell which is oriented in another direction. Or, in other words, the pitting is cross-matched. The opposing cell wall may have transversely or obliquely oriented pits. In *Angiopteris*, the *ob-scalariform pitting*, as it is proposed to call it, is more often near the end of a tracheid (Fig. 63), however, one can occasionally find such pitting elsewhere. Similar pitting has been observed in the Ophioglossaceae and in leptosporangiate ferns (*see* below). *Ob-scalariform pitting* is not to be confused with irregular reticulations which tend to occur in many plant groups in near isodiametric elements occurring near ends of vascular strands, e.g. leaf veins.

Tyloses frequently form in the protoxylem of the three genera of the Marattiaceae studied. In *Angiopteris* they are most extensive, eventually filling essentially all of the protoxylem elements and the earliest metaxylem elements. These have been referred to by McNicol (1908).

The tracheary elements of the Marattiaceae are generally referred to as being comparable to those of the Filicales (Eames, 1936; Bliss, 1939) with "typical" scalariform elements in the metaxylem.

OPHIOGLOSSACEAE — The early protoxylem elements of the Ophioglossaceae show striking similarities to those occurring in Marattiaceous genera. *Directly attached annular elements* occur in *Botrychium*, *Ophioglossum*, and also in *Helminthostachys*. The earliest elements of



FIGS. 49-65.

Botrychium (Figs. 66, 67) tend to have much finer thickenings than in comparable cells of *Ophioglossum* (Fig. 68) and *Helminthostachys* (not shown, but extremely similar to Fig. 68). *Directly attached annular elements* tend to grade into *annular-reticulate elements* and then into *reticulate elements* as in the Marattiaceae (Figs. 68-72).

Distinct helicoid thickenings occur in the Ophioglossaceae, but are quite uncommon. Elements with simple helical thickenings are entirely absent, but elements in which there is a helical band which is itself in the form of a reticulum do occur. Elements of this sort are here referred to as *reticulated helical*, not to be confused with *helical-reticulate* in which the reticulum is present between the gyres of a helix. In the more typical *reticulate elements* of the Ophioglossaceae a helical organization is often suggested.

In later formed reticulate elements of the Ophioglossaceae, openings in the secondary wall network usually do not tend to become restricted to cell faces. In *Ophioglossum* (Fig. 81) there is a trend toward reticulate elements with transversely elongate, slit-like openings and even towards openings (often of variable size and shape) with more or less distinct borders (Figs. 87, 88, 95). Scalariform elements of the type present in the Marattiaceae are, however, absent. Note the *ob-reticulate* arrangement of openings in Figs. 87 and 88. The element shown in Fig. 95 from the stem of *Ophioglossum vulgatum* represents the closest approach to the Marattiaceous type of scalariform element observed. In fact, only in the stem of this species was there observed a strong tendency for transversely elongate openings in a reticulum to be restricted to cell faces. These elements are illustrated and referred to as scalariform by Wright (1920, *see* her Fig. 7).

Distinctly bordered, more or less circular pits are a pronounced feature of the early and late formed tracheary elements of the three genera of the Ophioglossaceae. They are absent from the first formed protoxylem elements, but do appear in the protoxylem reticulate elements and later elements (Figs. 70, 71, 76, 77). In these elements there is a thick, unlignified primary wall, but the pit closing membranes are quite thin (Figs. 74, 78, 79, 80). The thick primary wall is clearly primary since it becomes thickened before the elements are stretched. The pit borders are usually formed by the lignified secondary wall; with the thickened primary wall not tending to overarch the pit chamber except to a very slight extent (*see* upper pit in Fig. 80). It seems justified to regard the thickened primary wall of the early tracheary elements of the Ophioglossaceae as the morphological equivalent of the "rims" or "bars" of Sanio, even though here it is in the form of a sheet and not a narrow bar or ridge. What is regarded as a comparable thickening in the Osmundaceae and in the Marattiaceae is mostly in the form of ridges on the primary base wall, but may fan out to some extent when secondary thickening strands unite.

In *Botrychium*, however, in the late protoxylem or early metaxylem pit pairs are present in which the base wall (presumed primary in this case) encloses the chamber (Fig. 82) and over which strands of the secondary thickening are present. A distinct border is formed by surrounding major thickenings of the secondary wall (Figs. 75, 82). Pit apertures in this could not be observed. In *Helminthostachys* a somewhat similar kind of a pit was observed, but without the extra

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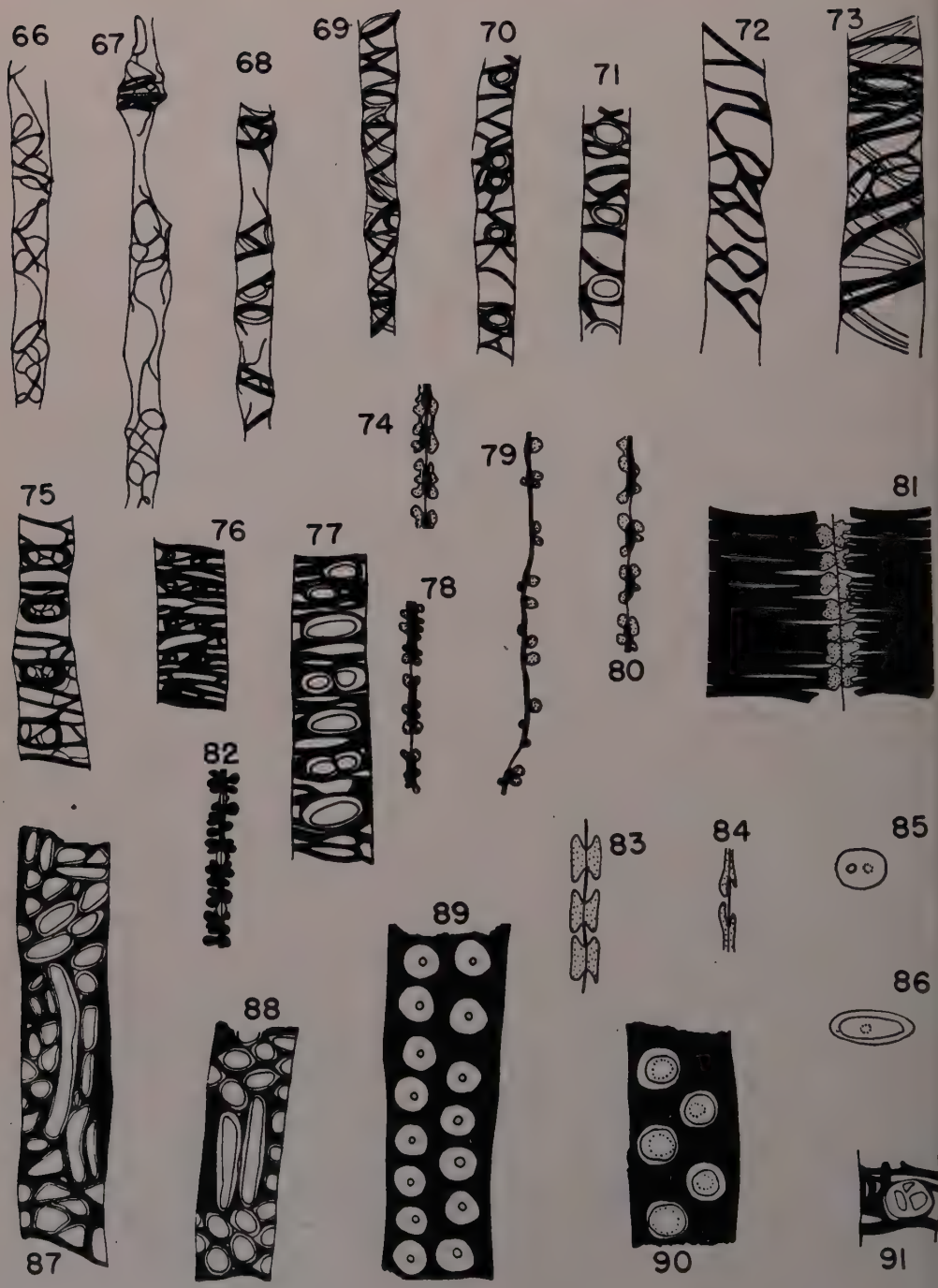
FIGS. 49-65 — Figs. 49-55. Portions of tracheary elements from the leaf of *Marattia alata*. × 666. Figs. 56-65. *Angiopteris evecta*. Fig. 56. Portion of a late protoxylem element. × 666. Fig. 57. Portion of Fig. 56 enlarged. Fig. 58. Sectional view of the wall of a late protoxylem element. × 666. Fig. 59. Portion of a late protoxylem element. × 666. Fig. 60. Portion of one of the latest protoxylem elements. This element is actually slightly stretched. × 666. Fig. 61. Portion of an element from the mid to late metaxylem. × 666. The broken line in Fig. 60 and in Fig. 61 represents a cell edge. Fig. 62. Sectional view of the walls of two adjacent scalariform elements. × 666. Figs. 63-65. Portions of scalariform elements from the metaxylem. × 666.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FIGS. 66-91.

strands of secondary wall material running over the outside of the chamber, and with several clearly defined apertures (Fig. 91).

The late metaxylem elements of the rachis of *Helminthostachys* show no more signs of reticulate structure, but merely a lignified secondary wall which is pitted in an alternate fashion (Figs. 83, 89, 90) on the inside of a very thin primary wall which is also lignified (except in the pit closing membranes) when the cell is matured. The opposing pit apertures of pit pairs in these elements are often of a very different size (Figs. 84, 86) and occasionally not in the center of the overarching part of the secondary wall (Fig. 85).

The late metaxylem elements of the stems of *Botrychium*, *Ophioglossum*, and *Helminthostachys* and the " secondary " xylem of the stem of *Botrychium* characteristically show irregular thickening and often differential patterns of lignification in their secondary walls presenting some sort of reticulate pattern in face view (Figs. 92, 94, 97). In all three genera these elements possess a relatively thick unlignified primary wall (Figs. 93, 96, 98). The secondary walls of these elements in *Ophioglossum* tend to be uniformly lignified, but irregularly thickened on their inner surfaces (Fig. 98). The thickened, unlignified and differentially stained primary wall gives to the surface view a reticulate aspect with bordered pits between (Fig. 97). The pattern shown in black in Fig. 97 is interpreted as the system of " rims of Sanio ", shown in sectional view in Fig. 98. Differential thickening makes the pits in comparable elements of *Helminthostachys* appear to be in valleys within the secondary wall (Fig. 94). In *Botrychium*, both differential thickening and pronounced differential lignification are present (Fig. 93), again giving the face view of the element a strong reticulate aspect (Fig. 92).

The term " tertiary " wall has been applied to certain wall layers of tracheids of the three Ophioglossaceous genera (Wright, 1920; Loughridge, 1932). The term seems unnecessary and unjustified.

Considerable attention was given to the pit closing membrane in the Ophioglossaceae, since a torus has been reported to occur in each of the three genera (Wright, 1920). Occasional thickened membranes were observed in the stems of *Helminthostachys* and *Ophioglossum* and frequent ones in the stems of *Botrychium*, but membranes which were differentially thickened as in a torus were found only in *Botrychium dissectum* and here their occurrence was not constant. In view of these discrepancies in observations, it is possible that the torus within the family may be an eratically occurring feature.

In *Botrychium*, the unlignified primary wall, or more accurately the compound middle lamella, tends to be thicker around the edges of the pit chamber (Fig. 93, top; Fig. 100). This rim of thickened unlignified wall can be seen distinctly in face view of the pit (Fig. 99) and is considered

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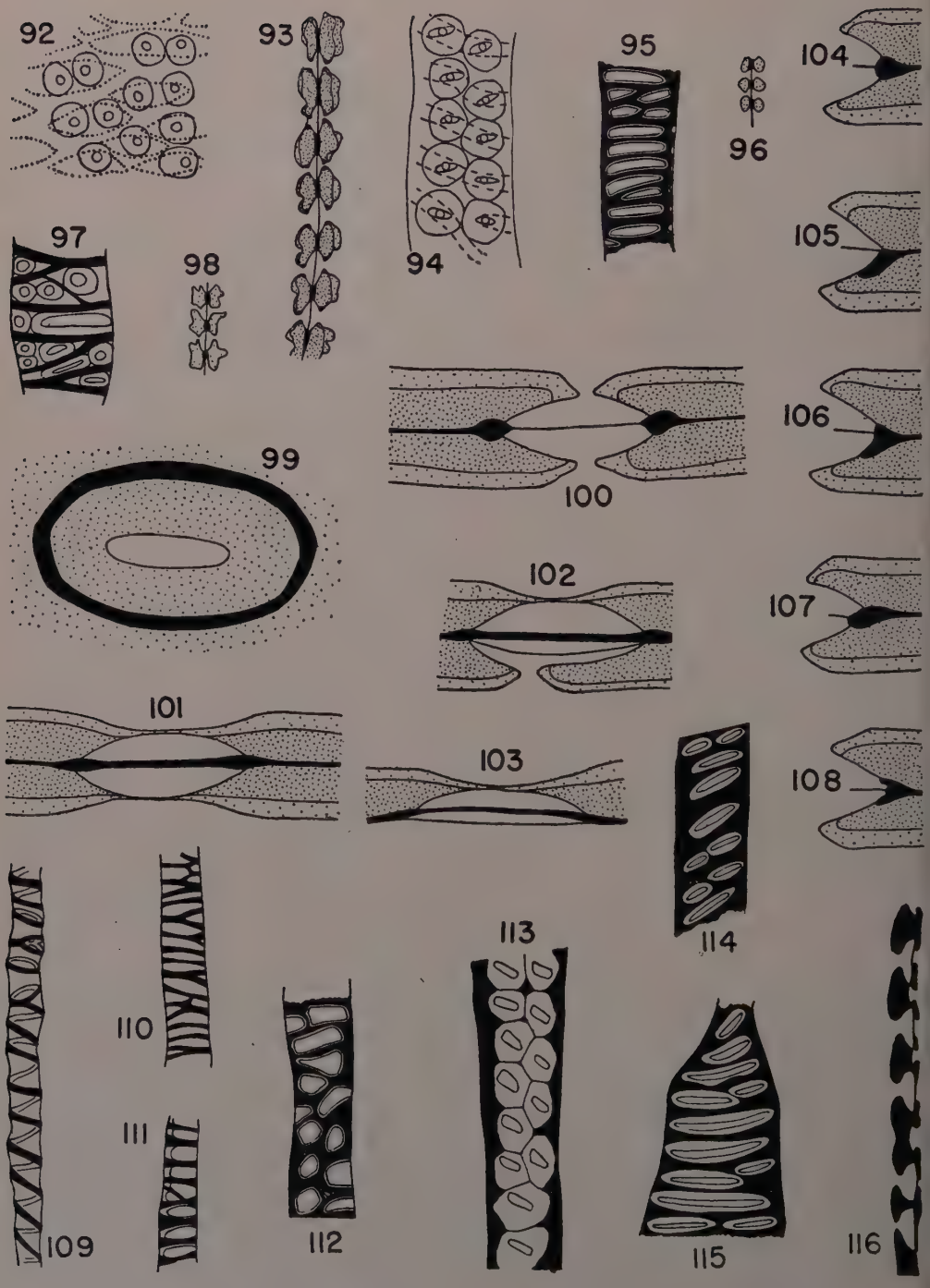
FIGS. 66-91 — Figs. 66, 67. Portions of tracheary elements from the petiole of *Botrychium multifidum*. × 666. Fig. 68. Same from the stem of *Ophioglossum pendulum*. × 666. Fig. 69, 70. Same from the petiole of *Botrychium multifidum*. × 666. Figs. 71, 72. Same from the leaf of *Ophioglossum vulgatum*. × 666. Fig. 73. Same from the petiole of *Botrychium simplex*. × 666. Fig. 74. As Fig. 73, sectional view of double wall. × 666. Figs. 75, 76. Portions of tracheary elements from the petiole of *Botrychium multifidum*. × 666. Fig. 77. Same from petiole of *B. simplex*. × 666. Figs. 78-80. Sectional views of portions of pairs of adjacent tracheary elements from the petiole of *B. simplex*. × 666. In Figs. 74, 78-80, stippled areas are lignified, blackened areas are unlignified. Fig. 81. Portions of two adjacent elements of the stem of *Ophioglossum pendulum*. × 666. Fig. 82. Sectional view of a portion of an early metaxylem element of *Botrychium multifidum*. × 666. Fig. 83. Sectional view of portions of walls of adjacent tracheary elements in the late metaxylem of *Helminthostachys* petiole. × 666. Figs. 84-86. Pit pairs in the late metaxylem of the petiole of *Helminthostachys* showing unequal opposing apertures. × 666. Figs. 87-88. Portions of elements in the metaxylem of the leaf of *Ophioglossum vulgatum*. × 666. Figs. 89-90. Same from the petiole of *Helminthostachys*. × 666. The dotted lines in Figs. 85, 86, and 90 represent the pit apertures of the opposing pits. Fig. 91. Portion of an element in the late protoxylem of the petiole of *Helminthostachys* showing a pit with three apertures and the pit truss. × 666.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FIGS. 92-116.

here as by Wright (1920) to be the morphological equivalent of the Rim of Sanio. Its shape in sectional view varies considerably (Figs. 104-108). It may appear as a symmetrical (Fig. 104) or an assymmetrical knob (Fig. 107) or it may extend outward and actually form part of the pit border (Figs. 105, 106, 108). It may even appear to extend slightly out onto the pit closing membrane (Figs. 100, 104, 107, 108). A sectional view of a pit pair at a non-median optical plane will show the unlignified rim suggesting a thickened pit closing membrane (Fig. 101). If the optical plane is slightly tilted both the rim and the true pit closing membrane may be seen (Figs. 102, 103). In the opinion of the author this is what is represented by the so-called "double membrane" of Wright (1920).

Tyloses occur in *Botrychium* and *Ophioglossum* in the early protoxylem. These have been referred to by McNicol (1908). They are not as extensively formed as in the Marattiaceae or in the Filicales.

The presence of bordered pits in the protoxylem elements of the Ophioglossaceae has been reported by Esau (1953). Nozu (1956), aware of Esau's report, could not recognize them in his material. The report of Esau was not particularly clear. She enumerated various plant groups in which bordered pits occur in protoxylem elements and indicated "and possibly Ophioglossales".

Loughridge (1932) described the protoxylem of the Ophioglossaceae as being composed of spiral and scalariform elements. Nozu (1956) reports the tracheids exhibiting spiral and scalariform markings on their walls "as in most ferns". Halle (1875) describes *Botrychium* as possessing spiral, netted to "leiterförmig", and bordered pitted elements and *Ophioglossum* as having mostly "leiterförmig" elements. Farmer & Freeman (1899) reported in *Helminthostachys* the presence of tracheids with bordered pits, oval or almost circular, and also tracheids "in which the pits assimilate the more scalariform type met with in other members of the family." Petry (1914) described from *Ophioglossum pendulum* elements with spirally and reticulately thickened walls.

OSMUNDACEAE — The early elements of the Osmundaceae show some similarities to those of the Ophioglossaceae and the Marattiaceae. The earliest elements are annular with some interconnections (Figs. 117, 118, 125). The interconnections are of approximately the same thickness as the rings themselves and they more often suggest portions of helices than corresponding elements of the Ophioglossaceae. In the stem, succeeding elements (Figs. 119-121) strongly suggest Ophioglossaceous and Marattiaceous types save for the absence of bordered pits. Compare Fig. 119 with Figs. 50 and 69. Figure 119 is a reticulate element, still with some suggestion of rings here and there. The later elements shown in Figs. 120 and 121 are protoxylem reticulate elements. In the

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FIGS. 92-116 — Fig. 92. Portion of an element from the late metaxylem or "secondary" xylem of *Botrychium virginianum*. Fig. 93. Same as Fig. 92, but sectional view of wall and opposing wall. Fig. 94. Portion of an element of the late metaxylem of the stem of *Helminthostachys*. Fig. 95. Same from the stem of *Ophioglossum vulgatum*. Fig. 96. Sectional view of the wall of the element shown in Fig. 95 and the opposing wall. Fig. 97. Portion of an element of the metaxylem of the stem of *Ophioglossum vulgatum*. Fig. 98. Sectional view of a part of the wall of the same cell as shown in Fig. 97, and the opposing wall. Figs. 99-108. *Botrychium virginianum*, "secondary" xylem. Fig. 99. Face view of a pit. Fig. 100. Sectional view of a pit pair, median optical. Fig. 101. Sectional view of a pit pair, non-median optical. Fig. 102. Sectional view of a pit pair, slightly oblique orientation with respect to optical plane. Fig. 103. Sectional view of a bordered pit and the adjacent primary wall of a parenchyma cell, slightly oblique orientation with respect to optical plane. Figs. 104-108. Sectional views of the edges of pit pairs. In Figs. 93, 96, 98, and 100-108, the blackened areas are unlignified, the densely stippled areas are weakly lignified, and the less densely stippled areas are strongly lignified. The dotted network shown in Fig. 92 indicates the face view appearance of the inner, strongly lignified parts of the wall shown in Fig. 93. Figs. 109-116. Elements of *Cycas revoluta*. Figs. 109-111. Taken from young leaf raches. Figs. 112-116. Taken from the axis of a "bulb" or adventitious shoot. Figs. 92-98, 109-116. × 666.


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FIGS. 117-137.

leaf, on the other hand, the helical pattern is well expressed (Figs. 126-128). The helical thickenings are relatively simple, but are single here, double there, and still multiple elsewhere, as the bands divide and recombine. There are, however, in the early helical elements few or no anastomoses between adjacent gyres. In other words, the elements may be stretched out, their helices uncoiled without rupturing any of the secondary strands. Occasionally several distinct and separate helical thickenings will run parallel for a distance in a given element (Fig. 128). Later helical elements in the protoxylem appear reticulate in face view (Fig. 130, 131), but are really helical in gross organization. In addition to forks, there are also a few anastomoses.

For describing the simpler types of helical elements the following nomenclatural proposals are presented: A *fork* in the helical system is intended to refer to a branching of a helical band to produce two helical bands. An *anastomosis* is intended to mean an interconnection between adjacent gyres, or in other words, a strand which would necessarily rupture if the helical system were to be stretched sufficiently. When viewing one side of an element, the *forks* are not distinct from the *anastomoses*; the distinction becomes apparent only when the three dimensional aspects of the helical system are taken into account. The term *singly helical* is meant to describe elements with a single helical band, similarly *doubly helical* for elements with two such bands, and *multiple helical* for those with more than two. The expression *singly-doubly helical* is presented to describe an element in which the helix is single at one point then forks to become double then recombines to become single again. The latter type of helical element occurs in its most diagrammatic form in each of the three Gnetalean genera.

The transition from early reticulate to scalariform in the Osmundaceae is similar to that in the Marattiaceae. Some differences, however, deserve to be mentioned. The early reticulate elements are essentially identical in both families. As will be seen below, the same comparison can be made with the early reticulate elements of the higher Filicales. In the later reticulate elements of *Osmunda*, the restriction of openings in the network to cell faces is long delayed and even in the last formed scalariform elements it is incomplete, so that both trans-edge alternate and trans-edge opposite pitting are to be found (Figs. 135-137). A considerable amount of heterogeneity is to be found in the intermediate reticulate elements; that is, thickenings of various sizes, some rather thin as compared to others (Figs. 123, 131). Figure 131 is actually a helical element, but it illustrates the kind of heterogeneity also found in some of the reticulate ones. Interconnections between converging strands usually show the extended groove which tends to separate on stretching of the element as in the Marattiaceae.

Patterns of lignification in early elements deserve mention. The earliest elements of the Osmundaceae show the annular or helical thickenings with a pronounced unlignified core which is overlain with a thin lignified wall which is continuous not only over the thickening, but also over the continuous base wall. Its inner surface tends to be somewhat irregular (Fig. 133). In the later protoxylem elements the inner lignified wall is more massive and its irregularities are accentuated (Fig. 134). There is a slight border (overarching),

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FIGS. 117-137 — Portions of tracheary elements of *Osmunda cinnamomea*. Figs. 117-124, 135-137, from stem. Figs. 125-134, from leaf. Figs. 117-131, 135-137. × 666. The element shown in Fig. 129 is a helical element. The sections through the gyres are shown in black and were lignified. The inner wall shown clear was unlignified. Fig. 132 is a portion of a helical thickening from another element showing a lignified core (blackened area). Fig. 133 is a portion of a helical thickening from one of the earliest protoxylem elements, again showing a lignified core (blackened area) and slight irregularities on the inner, unlignified wall. Fig. 134 is the same as Fig. 132, but enlarged and with additional details of wall irregularities shown. Figs. 133 and 134 are reproduced at the same scale.

FIGS. 138-147.

but a pronounced false border due to the unlignified core (Fig. 132).

Tyloses occur in the protoxylem of the Osmundaceae (Figs. 163, 165) as in families previously mentioned. The tyloses often enter one tracheid from adjacent parenchyma, expand and extend into yet another tracheid (Fig. 165) as described by McNicol (1908). The tyloses in *Osmunda* as well as in many other ferns extend into a protoxylem element between two adjacent thickenings and are thus restricted by the secondary thickenings on two sides only, but in cross-section the young tyloses are still circular (Fig. 163), not broadly eliptical as one might expect.

Previous references to the structure of the tracheary elements of the Osmundaceae are few and relatively uninforming. Faull (1901) refers to two kinds of wood elements in the family: small ringed and spiral elements in the protoxylem and scalariform tracheids in the metaxylem. Bliss (1939) ascribes to the Osmundaceae elements not markedly different from the fern genera with scalariform pitting and occasional " serial pitting ".

Higher Filicales — It seems pointless to discuss the tracheary elements of the Filicales family by family in view of the nature of the sample selected for this study. The " higher Filicales " as used here refers to all of the families of the order except the Osmundaceae. The sample taken might be considered highly inadequate to characterize the group, however, the constancy with which certain characteristics are observed from genus to genus permits a limited amount of justified generalization. In addition, the information collected during the examination of the members of this rather meager sample will add materially to an overall interpretation of certain aspects of tracheary element morphology.

Copeland (1947) in his *Genera Filicum* recognizes 18 families in addition to the Osmundaceae in the order Filicales. Of these 18, 11 are included in the present study. The 25 genera and 27 species (*see* Materials and Methods) studied are distributed among the 11 families as follows:

Schizaeaceae, 2 gen. and 2 spp.; Hymenophyllaceae, 1 gen. and 1 sp.; Pteridaceae, 7 gen. and 7 spp.; Davalliaceae, 3 gen. and 3 spp.; Cyathaeaceae, 1 gen. and 1 sp.; Aspidiaceae, 4 gen. and 4 spp.; Blechnaceae, 2 gen. and 2 spp.; Aspleniaceae, 2 gen. and 4 spp.; Polypodiaceae, 1 gen. and 1 sp.; Marsileaceae, 1 gen. and 1 sp.; Salviniaceae, 1 gen. and 1 sp.

In the early protoxylem of the stems and raches of the higher Filicales, one typically finds loosely reticulate elements (Figs. 140, 148) similar to those found in the Osmundaceae. In the stems these elements are more often the first to mature. In leaves, however, they are preceded by annular and helical types. The annular elements when present occasionally possess an extensive series of simple separate rings, e.g. in the rachis of *Pteridium*, but more often are in part helical (Figs. 138, 139). Helical elements usually follow in the ontogenetic sequence the annular or annular-helical hybrid types, or they may be the first in the sequence. The helical elements are rarely if ever as diagrammatically simple as they often are in certain angiosperms, but possess rather frequent forks (Figs. 139, 149), and in the latter members of the helical series, anastomoses (Figs. 150, 151). In Fig. 151 opposite sides of the same cell are shown. It is clear that in the upper part of the portion of the tracheid shown the helix is simple, but toward the lower end forks and anastomoses produce a reticulate effect.

The protoxylem elements of most of the higher Filicales in the later ontogeny of the organ possess tyloses (Figs. 164, 166). The tyloses are often compound (Fig. 166), that is, they enter a tracheid from a

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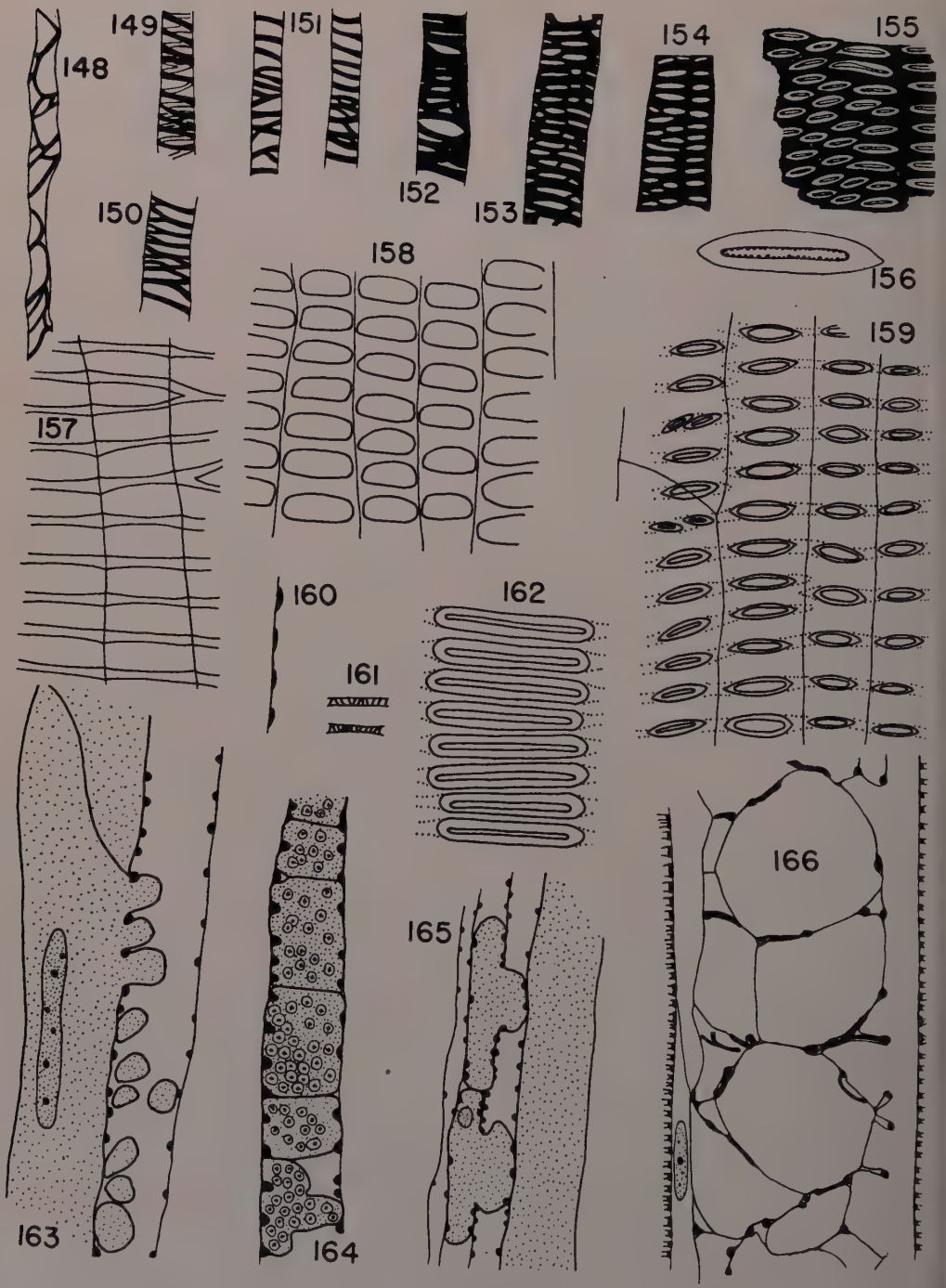
Figs. 138-147 — Figs. 138-144, 146, 147. Portions of tracheary elements of *Blechnum*. Fig. 142 is a cross-section of an element similar to the one shown in Fig. 146. The dotted lines in Figs. 143 and 144 indicate the continuity of thinner areas across cell edges, i.e. the valleys in which the pits are situated. Fig. 145. A portion of an element from the stem of *Dennstaedtia*. All × 666.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FIGS. 148-166.

parenchyma cell then enter another tracheid from the first one. This may be repeated several times as described by McNicol (1908). The tyloses often, especially in *Pteridium* raches, enlarge considerably and completely distort the region of the protoxylem (Fig. 166). A cross-section corresponding to Fig. 166 usually shows what appears to be several large "parenchyma cells" which is the "cavity parenchyma" of McNicol (1908). In the rachis of *Pteridium* the cavity parenchyma occupies a larger area than did the protoxylem since the tyloses form and enlarge before the surrounding tissues have fully expanded laterally. Gwynne-Vaughan (1908) who considered most fern tracheids to have lateral perforations rather than pits quotes Weiss (who reported tyloses in *Zygopteris* and *Rachiopteris*, Weiss, 1906) from her personal communications as saying that the presence of open passages in the side walls renders it easy to account for the tyloses he found far away from any living elements. In all instances in the present study the membranes were clearly observed. Weiss (1906) used the presence of tyloses as "confirmatory evidence" to indicate two petrified fern specimens, a stem and a rachis, were connected. In view of the almost general occurrence of tyloses in the early primary xylem of ferns this now seems quite unjustified. Molish (1888) described tyloses in a great variety of vascular plants, but could not detect them in any of the ferns which he examined; he however, studied only late metaxylem.

It will be recalled that in the Ophioglossaceae and in the Marattiaceae, the protoxylem elements show a large amount of heterogeneity in the thickness of the secondary thickenings within given cells as regards to a face view appearance of the cells. This kind of heterogeneity is expressed to a much lesser extent in the Filicales, with the Osmundaceae and the Schizaeaceae showing the greatest amount in the order. In *Schizaea* the heterogeneity is pronounced not only in a face view aspect (more accurately the width of the thickening), but also in the dimension along the radius of the cell (the depth of the band). In this genus the feature is expressed not only in the protoxylem, but also into the late metaxylem where a face view of a scalariform element at a given focal plane will give the impression that certain of the transverse bars are unattached at one or both ends to the rest of the secondary wall. Outside of the Osmundaceae and the Schizaeaceae within the Filicales, heterogeneity is unpronounced, but usually can be detected.

The ontogenetic sequence of tracheary types in the higher Ficales thus far described is (1) annular (or annular-helical), (2) helical, (3) loosely reticulate with either 1, 2 or 1 and 2 omitted from the sequence. The reticulate series which follows is somewhat similar to that found in the Osmundaceae (Figs. 141, 152, 153, 154). Complete restriction of openings in the reticulum to cell faces is not common in the higher Filicales. Occasionally one finds

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FIGS. 148-166 — Figs. 148, 150. Portions of tracheary elements from a young rachis of *Scholopendrium*. Figs. 149, 151. Same from stem of *Polypodium peroussum*. Figs. 152-154. Same from rachis of *Asplenium viride*. Fig. 155. Same from young rachis of *Onoclea sensibilis*. Fig. 156. One pit enlarged from Fig. 155. Figs. 157-159. Stages in the development of the wall of a vessel adjoining parenchyma cells of *Pteridium aquilinum*. The vertical lines may be considered to represent the edges of the vessel wall or the junctions between adjacent faces or sectional views of the walls of adjoining parenchyma cells the planes of which are at right angles to the plane of the paper. Fig. 160. Sectional views of the thickenings shown in Fig. 157. Fig. 161. Face view of two of the thickenings shown in Fig. 157 showing pattern of differential staining. Fig. 162. Portion of an element from the rachis of *Pteridium aquilinum*. The dotted lines represent the continuations of the valleys of the wall in which the pits are situated. Fig. 163. Portions of two parenchyma cells and an adjacent protoxylem element with a number of tyloses from the leaf of *Osmunda cinnamomea*. Fig. 164. A portion of a protoxylem element filled with tyloses from the stem of *Onoclea sensibilis*. Fig. 165. Tyloses in the protoxylem of *Osmunda cinnamomea*. Fig. 166. The protoxylem of an old rachis of *Pteridium aquilinum* completely disrupted by tyloses. Figs. 148-155, 157-166. × 666.

toward the end of the reticulate series elements in which the openings do not cross cell edges, but are trans-edge opposite (Fig. 154). This will be discussed below.

Scalariform elements with trans-edge opposite pitting seem to be of general occurrence among the higher Filicales. Trans-edge opposite pitting always occurs along with at least some trans-edge alternate pitting. This is observed with at least the same frequency as discontinuities are observed in the transverse rows of pits on the faces (if there is any opposite pitting on the faces) or with at least the same frequency as elongate pits end on the faces and are not opposite to adjacent ones. More often the frequency of occurrence of trans-edge alternate pitting in elements which are described here as having trans-edge opposite pitting is somewhat higher than the frequency of occurrence of row disturbances on the faces. This indicates that the tendency, which is so pronounced in the Marattiaceae for forks and anastomoses within the major framework of the secondary walls of these cells to become associated with cell edges, does occur to some extent in the higher Filicales and is to an extent intermediate between the Marattiaceae and the higher Filicales in the Osmundaceae.

That there is a major framework within the secondary walls of these elements upon which a pattern of pits is superimposed is brought out by the following evidence: The secondary wall is often clearly thinner between adjacent horizontal pairs of pits than between vertical pairs of pits. In other words the pits can be seen to occur in valleys of the secondary wall. When the valleys are seen, they are seen not only on the faces, but also across the cell edges (Figs. 143, 144, 159, 162). These valleys are relatively easy to detect in *Blechnum*, *Pteridium*, *Cibotium*, and *Dicksonia*, as examples. The differences in thickness between the secondary wall between the valleys and that within the valleys is often great enough so that by focussing deeper into the cell the pits can be taken completely out of focus and the major structural framework of the cell only can be clearly seen.

The larger pits are always oriented parallel to the sides of the valley. The shorter ones, however, may have their axes somewhat tilted and even overlap within a given valley (Figs. 144, 159). One occasionally sees in a fern tracheid a close series of such short pits (Fig. 155) arranged in what might appear an alternate fashion; but in view of the observations presented above, they must be interpreted as being opposite.

The valleys, interpreted here as homologs of reticulate openings, may be oriented from transverse to vertical. Oblique orientation of valleys in association with walls which are too thick to clearly observe the valleys leads to a false impression of trans-edge alternate pitting in cells in which the pitting is actually trans-edge opposite. Extremes in departures from transverse orientation occur in *Dennstaedtia* (Fig. 145) and *Blechnum* (Figs. 142, 143, 146, 147) where obscalariform elements are common. Where elongate pits are oriented obliquely to vertically, the opposing pits in the adjacent cell are usually cross-matched (Fig. 285).

Additional evidence for the existence of major structural frame-work of the secondary wall upon which the pitted pattern is superimposed comes from the ontogeny of vessel members in *Pteridium*. Figures 157-159 represent portions of three different vessel members of successive stages in maturity from the last formed metaxylem of the *Pteridium*. Only a portion of a single vessel member is shown in each figure; the vertical lines represent the edges of the vessels or the walls of parenchyma cells the planes of which are at right angles to the plane of the drawing. In the young vessel member one can see a helical to reticulate system of thickening bands which show no regard for cell edges and cell faces (Figs. 157, 160). They appear at a stage when the vessel member has reached its maximum diameter and when the edges and faces are established and fixed. The wall between the thickenings is quite thin both on the faces and on the cell edges. In face view the thickening often shows some vertical lines due to differential staining within the band (Fig. 161). Wall deposition procedes along the wall radiating from the original thickenings and especially along the cell edges, so that pit-like openings are soon

evident (Fig. 158). This process is continued by the formation of more wall substance until the mature bordered pit is formed. The valleys between the pits, both on the faces and across the cell edges, are still clearly seen in the mature cell (Fig. 159). Membrane breakdown associated with perforation plate formation occurs at a stage in the development of the end wall comparable to that shown in Fig. 158, not Fig. 159, so that one cannot say that these pits associated with pore formation become larger, but it must be stated that they fail to reach their mature smaller size. The development of intervascular pitting in *Pteridium* follows the same sequence of events described above, the pitting, however, is more broadly scalariform (Fig. 162). The spiral thickening which appears first in the vessel members of *Pteridium* can probably be referred accurately to " rims " or " bars " of Sanio.

Irregularities of the inner wall in the form of small projections, or vesturing, are common throughout many of the higher Filicales. These are illustrated for *Onoclea* in Fig. 156 which represents one pit enlarged from Fig. 155.

Throughout the higher Filicales small unlignified ridges at the base of the secondary thickening in the metaxylem elements are common. They may take the form of a single ridge in sectional view, similar to the one shown in Fig. 62, or a double one where each of the two surrounds the adjacent pit chamber, as shown for *Botrychium* in Fig. 100. In the Filicales they are never as pronounced as they are occasionally in *Botrychium*. These ridges may similarly be referred to as " Bars " of Sanio. Most of the earliest elements of the higher Filicales tend to have an unlignified primary wall with a more or less completely lignified secondary thickening.

Pit matching or pairing is variable in the metaxylem of certain higher Filicales. Pits in the faces of tracheary elements bordering parenchyma are more often without counterparts than paired. Some of the observations were made where the wall of the opposing parenchyma cell had enough thickness to avoid misinterpretation. Pairing in the intervascular pitting is also often not constant. It has already been mentioned above that pits which are oriented obliquely to vertically usually are cross-matched with pits in opposing walls. Even where the pits are transversely oriented in each of the opposing walls of adjacent elements, pairing may be irregular. In *Pteretis*, for example, one finds some ordinary pairing and in addition some scalariform pits which are matched with a vertical pair of pits in an adjacent cell. Sometimes this relationship is repeated regularly over a given face. A single elongate pit is often matched to a horizontal pair in an adjacent element, but this is a feature which occurs in most of the major groups of vascular plants.

There are numerous references to the structure of tracheary elements of the higher Filicales in existing literature. The late metaxylem scalariform element or scalariformly pitted element, as recent workers prefer to call it, has been generally ascribed to members of the group (Ogura, 1938; Atkinson, 1894; Bailey, 1925; Bower, 1923; Eames, 1936; Campbell, 1928; Prantl, 1875, 1881; Bliss, 1939; Boodle, 1901a, b; Ford, 1902; Gwynne-Vaughan, 1901; Link, 1841; Lange, 1891).

The spiral arrangement of pits and thus the trans-edge opposite arrangement was recognized by Link (1841), Bliss (1939), and Gwynne-Vaughan (1901). The latter two authors referred also to the way in which the fern tracheids split along a spiral line when treated with Potassium hydroxide as also did Russow (1872), which is referable to the overall framework of the cell walls.

The early xylem (proto- and early meta-) has similarly been described on a number of occasions, but descriptive terms were used without adequate illustrations so that it is rather difficult if not at times impossible to be certain of the way in which certain terms were used. Ambiguity in terminology is made clear in the table included in the discussion. Here it could be pointed out that " annular " has often been used to describe unstretched helical elements; " helical " has been used to describe unstretched annular elements and simple reticulate elements; " reticulate " more often has been used in the ferns to refer to early metaxylem elements and not to the simple reticulate elements

of the protoxylem (this is a guess); " scalariform " has been used to describe unstretched helical elements, simple reticulate elements, metaxylem reticulate elements with transverse openings, and also scalariformly pitted elements. The following descriptions are available: Ogura (1938) — the early xylem elements of ferns in general show ring- to spiral-form thickenings, later xylem is scalariformly pitted; Atkinson (1894) — in ferns generally there are spiral, reticulate, and scalariform tracheids; Bailey (1925) — " In the metaxylem of the Filicales, the scalariform reticulate thickenings frequently acquire overhanging margins and thus form transversely elongated pits . . . "; Bower (1923) — in ferns the tracheids of the protoxylem are spiral or reticulate as in most other vascular plants, scalariform tracheids in the metaxylem; Campbell (1928) — first elements are spiral or reticulate, later ones are large scalariform elements; Prantl (1875) — in Hymenophyllaceae, early xylem composed of reticulate elements, later ones scalariform; Prantl (1881) — the protoxylem is scalariform in *Schizaeae*, reticulate in other genera of *Schizaeaceae*, later elements in the family are scalariform; Boodle (1901) — in *Schizaeaceae*, the xylem elements are spiral, annular and scalariform; early xylem of the stem of *Lygodium* is finely scalariform; Boodle (1901b) — in *Gleichenia*, the early elements are annular and spiral, later ones scalariform; in some species all are scalariform; Chang (1927) — protoxylem elements of *Pteridium* are spiral; Demalsy (1953) — protoxylem elements of *Azolla* are spiral; Ford (1902) — protoxylem elements of *Ceratopteris* are spiral, later ones scalariform; Gwynne-Vaughan (1901) — protoxylem of *Loxsoma* composed of scalariform elements as is later formed xylem; Lange (1891) — elements of *Aspidium* are spiral, netted, and scalariform.

Cycadaceae — In all the three genera of the Cycadaceae studied, the earliest elements were annular-helical hybrid types (Fig. 109). The helical portions tended to be mostly simple and single. An occasional fork and portion of a double helix could, however, rarely be found. The rings were simple or occasionally forked. A helical to reticulate series followed with reticulate elements appearing in the protoxylem, but not as early in terms of elongation of the organ as in the ferns. In other words they were only slightly stretched (Fig. 110). Some of the intermediate protoxylem elements possessed a secondary-secondary wall as in the Psilotaceae (Fig. 111). Later reticulate elements possess broad openings which traverse cell edges (Fig. 112) and grade into (in *Cycas*) a kind of pitted element with crowded pits which have broad angular borders and irregular although usually elongate and angular apertures (Fig. 113). This kind of pitted element preceded the scalariform element in the metaxylem of the stem of *Cycas*. The scalariform elements which can be found in the primary xylem of *Cycas*, *Dioon*, and *Ceratozamia* have pits with broad borders and wide apertures (Figs. 114, 115). The elongate pits of the metaxylem are oriented obliquely to transversely in the cell walls (Figs. 114, 115); they have never, however, been observed to approach vertical orientation. Pitting is primarily trans-edge opposite, this being difficult at times to determine due to oblique orientation of pits and rows of pits and also due to slight offsetting of adjacent pits in a row both on faces (Fig. 115) and across edges. Pit matching between protoxylem and metaxylem tracheary elements and parenchyma is often irregular (Fig. 116).

The following descriptions of early formed primary xylem elements of the Cycadaceae have appeared in the literature: Von Mohl (1832) mentions the occurrence of spiral elements and their modifications. Warburg (1883) describes scalariform cells which on stretching acquire the appearance of netted cells as the openings change from slit-like to more nearly rectangular. These are the protoxylem reticulate elements described above. Sifton (1915) described the primary ridges of cycad elements and referred to them as " bars of Sanio." Sifton (1920) characterized the protoxylem of cycads as spiral and scalariform and described the pitting in later formed elements in some detail. Penhallow (1907) described the early protoxylem as being

composed of spiral elements, and later ones of more compact structure with points of coalescence, and still later ones as scalariform, but still retaining more or less the lines of the original spiral. Bailey (1925) referred to cycad early formed xylem as scalariform reticulate, with later formed elements with more conspicuously bordered meshes which in still later formed elements break up into smaller bordered pits of opposite or alternate seriation. Chrysler (1937) refers to the presence in *Zamia* of scalariform reticulate elements in the protoxylem and scalariform elements in the later formed xylem, and in *Stangeria* of scalariform and spiral elements in the protoxylem.

GINKGOACEAE — The earliest elements to mature in *Ginkgo* are very narrow annular elements (Fig. 167). The rings are simple, separate, lignified and rather thin. The primary wall is delicate and unlignified. These elements are followed in the ontogenetic sequence by slightly larger annular elements with thicker rings which are here and there interjoined by vertically or obliquely oriented strands of thickening (Fig. 168) or by elements of an annular-helical hybrid type (Fig. 169). The helical portions may be single or double (Fig. 169). Single helical portions may terminate with a ring (Fig. 169, third ring from the top). Double helical portions may also terminate with a ring or the two thickenings may fuse to a single one (Fig. 169) or the two thickenings may be terminated by a simple direct connection (Fig. 169, bottom). The latter feature seems to be especially uncommon in non-seed bearing vascular plants. Rings may be forked (Fig. 170) with the two lips of the double portion usually being close together.

The following elements in the sequence are helical (Figs. 171, 172). The helices have never been observed to be uniformly single, double or multiple. On the contrary, they show frequent points of branching so that the elements are singly-doubly (to multiple) helical (Fig. 172). When only one side of such an element (Fig. 171) is considered, it strongly suggests a reticulate element or a helical element with forks and anastomoses, but as far as could be determined, if the elements shown in Fig. 171 were to be stretched out completely, there would be no points of rupturing until the helix itself was straightened. There is often some degree of heterogeneity among the individual thickenings (Fig. 171). The transition of elements up to this point was seen much abbreviated in the short shoots and in the cotyledons.

The helical elements are followed by a helical to reticulate sequence. The early elements of the sequence suggest singly-doubly (to multiple) helices with frequent anastomoses (Fig. 173), the later ones being quite reticulate (Fig. 174). The first bordered pits appear in this sequence (Fig. 174).

Successively later formed elements show progressively smaller openings in the reticulum (Figs. 175, 176) until finally all suggestions of the reticulum are lost. It is suggested that the expression *tangential wall filling* be used to describe these events shown by the sequence of cell types. Similarly *centripetal wall filling* which can be detected in *Ginkgo*, especially in the cotyledons, is proposed to describe the sequence of changes from reticulate to pitted where the openings in the reticulum become progressively shallower, but not necessarily narrower as seen in face view, until the inner surface of the wall toward the end of the sequence is essentially smooth.

In discussing changes in the structure of tracheary elements it is necessary to distinguish among three kinds of changes. This may appear elementary and obvious to many readers, but a superficial examination of the literature quickly reveals frequent ambiguity. Firstly, there are *ontogenetic changes* which are undergone by individual cells during their existance. An example of such a change would be the change from helical or helical-reticulate to pitted of the vessel member of *Pteridium*. Secondly, there are *sequential changes*. These are the changes from one element to the next in an ontogenetic sequence of cell types, as for example the changes from helical through reticulate in several plant groups. Thirdly, there are *phylogenetic changes* which are interpretations that may be based in part on the other two types of changes as well as evidence from elsewhere.


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Figs. 167-192.

Bailey (1925) mentions the occurrence of circular bordered pits in early formed elements of *Ginkgo*, and also sporadic occurrence of elongate bordered pits. His interpretations resulting from these observations will be considered in a later section. Gunkel & Wetmore (1946) describe the early formed elements of *Ginkgo* as helical or rarely annular, with helical elements grading into circular bordered pitted types. They also mention the presence of bordered pits in early formed elements between the turns of the helical thickening.

TAXACEAE — The early elements in the ontogenetic sequence of *Taxus* are annular-helical hybrid types (Fig. 177). Forks in the helical thickenings occur commonly in the earliest elements resulting in rather short lengths of double helices (Fig. 177). Singly-doubly (rarely to multiple) helical elements follow (Fig. 178) with occasional anastomoses (Fig. 179). Bordered pits appear here in the sequence and are therefore earlier in the ontogenetic sequence than in *Ginkgo*. Heterogeneity among the thickenings can be detected, but it is not pronounced (Fig. 179). The primary wall of the early helical elements often tends to be appreciably thick (Fig. 180), but unlignified and is stretched to some extent.

Later helical elements show forks and some anastomoses, but the helical pattern remains evident. Figure 181 shows opposite sides of the same portion of an element from the stem of *Taxus*. If the two figures are mentally superimposed, the helical pattern becomes clear. Figure 182 shows a similar element from the axis of the female "strobilus". The elements shown in Figs. 181 and 182 were still part of the protoxylem as evidenced by the facts that they possessed unlignified primary walls and were found in incompletely elongated regions.

Later formed helical elements are similar in face view to those shown in Figs. 181 and 182. They illustrate *centripetal wall filling*, however, with an appreciable amount of secondary wall material over the entire inner surface of the cell, but considerably thicker in bands (Figs. 183, 184) giving to the surface view a pattern similar to the earlier elements of the sequence. *Tangential wall filling* is only slightly evident in *Taxus*. This can be seen if one compares Fig. 181 with Fig. 185 which is a reticulate element in the late metaxylem. Figure 187 shows a further stage in *centripetal wall filling* and is a sectional view of the wall of the same cell shown in Fig. 185. *Centripetal wall filling* is not complete in *Taxus*, but toward the end of the metaxylem sequence and into the secondary xylem the tracheids show the so-called "tertiary" thickening (Fig. 186).

CONIFERALES — The ordinal name Coniferales as used here excludes the Taxads, following the opinion of Florin (1951). The variation from family to family within the Coniferales is not appreciable. The differences between the Taxaceae and the Coniferales are not very great as will be appreciated, but among the conifers the difference from family to family is of an even lesser order of magnitude. For this reason, only the elements of *Pinus* are illustrated and described in detail.

The earliest protoxylem elements of *Pinus* are helical (Figs. 188-191) with thin unlignified primary walls. The helices are never diagrammatically simple and rarely single. They show frequent forks

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FIGS. 167-192 — Figs. 167-176. Portions of tracheary elements from the long shoot (2-year old seedling) of *Ginkgo biloba*. × 666. Figs. 177-179. Portions of tracheary elements from the stem of *Taxus baccata* (*sens. lat.*). Fig. 179 shows views of opposite sides of the same cell. × 666. Fig. 180. Sectional view of the wall of the same cell shown in Fig. 179. × 1660. Fig. 181. Views of opposite sides of the same tracheid from the stem of *T. baccata*. × 666. Fig. 182. Portion of a tracheid from the axis of the female "strobilus" of *T. baccata*. × 666. Figs. 183, 184. Sectional views of walls of late helicoid elements from the stem of *T. baccata*. × 1660. Figs. 185, 186. Portions of tracheids from the stem of *T. baccata*. × 666. Fig. 187. Sectional view of the wall of the cell shown in Fig. 185 and opposing wall of the adjacent cell. × 1660. In Figs. 180, 183, 184, and 187, stippled areas are lignified, blackened areas are unlignified. Figs. 188-192. Portions of tracheary elements of *Pinus mugho*. × 666. Figs. 188, 189, 191, 192 from a young long shoot; Fig. 190 from the female cone axis.

FIGS. 193-208.

and therefore vary in their degree of multiplicity (Figs. 188, 190, 191). Some of the relatively early (but not earliest) elements show extra irregularly disposed interconnections and therefore tend somewhat to be reticulate. The multiple helical elements or multiple helical with a somewhat reticulate tendency on complete stretching (Fig. 192) tend to leave close bunches of wall thickenings here and there separated by completely flattened portions of the cell through which one to several strands are continuous. Suggestions of annular thickenings are rare in *Pinus*.

The circular bordered pit appears in the protoxylem elements of *Pinus* (Figs. 188, 189, 191) at a stage in the ontogenetic sequence somewhat earlier than in *Taxus*, but among the other Coniferales there is some variation in this respect. Among the conifers, however, they seem never to appear in the sequence as late as they do in *Ginkgo*.

As in *Taxus*, the late helical members of the ontogenetic sequence show pronounced *Centripetal wall filling* (Figs. 195, 197). The base wall on the inner surface of which is superimposed the helical pattern may occasionally be unlignified even well into the helical thickenings (Fig. 197). In most other conifers, the entire base wall as well as the helical thickenings is usually entirely lignified. In *Pinus*, well into the metaxylem, the entire wall is similarly lignified (Fig. 195).

The helical pattern becomes lost or obscure as *centripetal wall filling* progresses in the ontogenetic sequence (Fig. 194).

In addition to *centripetal wall filling*, *tangential wall filling* is expressed in *Pinus* as well as in most other conifers. This is illustrated in Fig. 196.

The early formed tracheary elements of conifers are referred to in several previous publications. Penhallow (1907) states that spiral tracheids are typical of the protoxylem of all genera showing a more or less definite tendency of the spirals to coalesce here and there. Thompson (1914) describes the primary xylem of *Araucaria* as containing " ringed, spiral, and scalariform " elements as well as " transitional scalariform " elements which he described as scalariform elements which show signs of becoming typical multiseriate bordered pitted. Pool (1929) refers to *Araucaria* as having spiral tracheids with one, two or less frequently three spiral thickenings and thin primary walls which become irregularly stretched in the protoxylem and tracheids with 3 to 6 close spiral thickenings and thin primary walls in the metaxylem. Crafts (1943) describes *Sequoia* as having tracheids with single spirals in the early formed xylem and double or more complex spirals in the later formed xylem. Jeffrey (1912) speaks of scalariform elements in the protoxylem of *Araucaria*.

The presence of circular bordered pits in the early wood of conifers was described by Bailey (1925), but was illustrated earlier by Hartig (1878) and Jeffrey (1917). Later, Crafts (1943) refers to them in *Sequoia*, Buchholz (1933) in *Cedrus*, and Pool (1929) in *Araucaria*.

Ephedraceae — The earliest elements of *Ephedra* have thin unlignified primary walls internal to which is a series of diagrammatically simple rings with, in some cases, an occasional interconnecting gyre (Fig. 205). Succeeding elements are less annular and more helical (Fig. 205) and still later ones are entirely helical.

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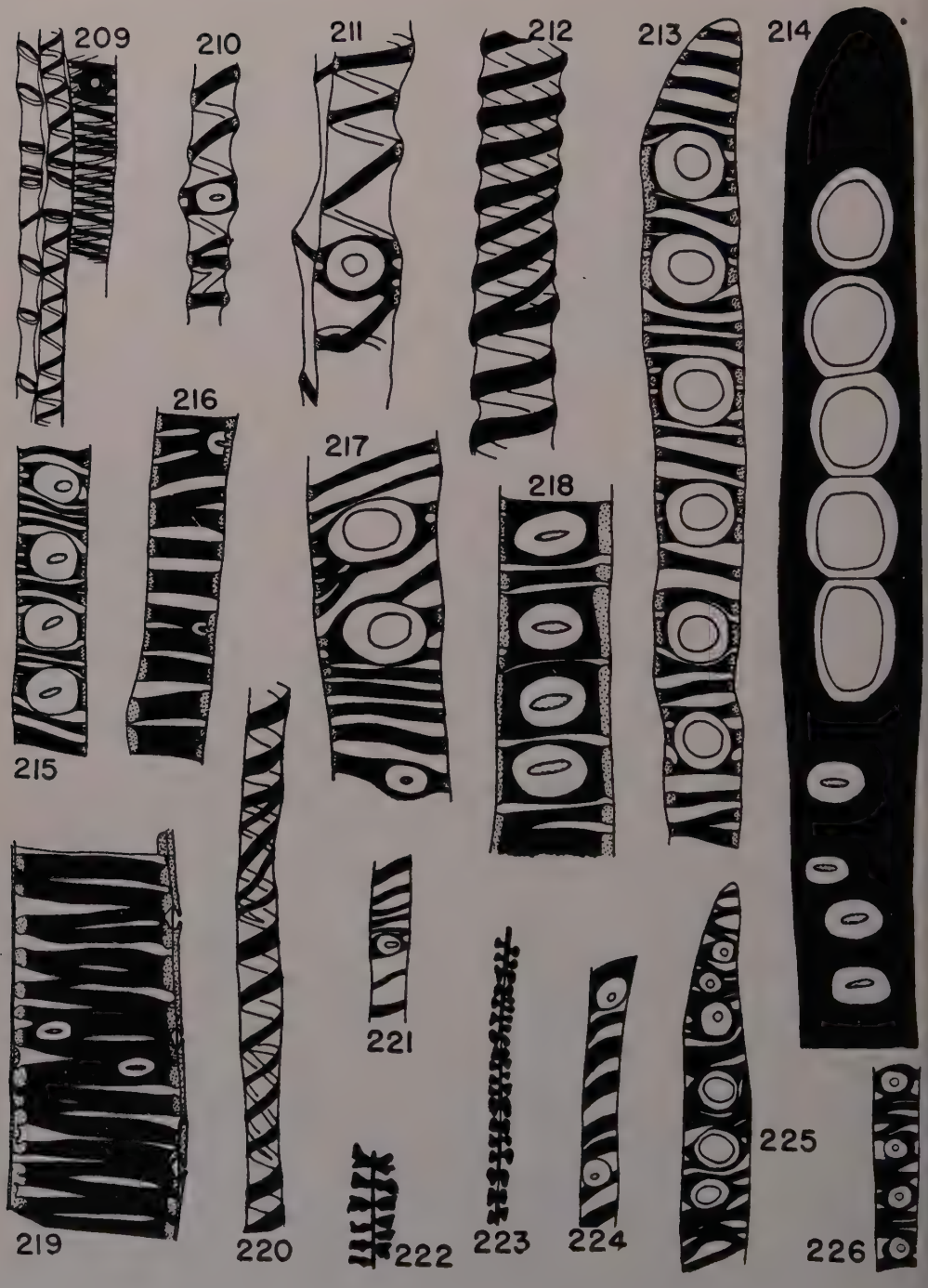
Figs. 193-208 — Figs. 193-197. *Pinus mugho*. Figs. 193, 194. Portions of tracheary elements from the long shoot within the region of elongation and from the female cone axis respectively. × 666. Fig. 195. Sectional views of the walls common to two tracheids from the metaxylem of the female cone axis. These elements were reticulate in appearance in surface view. × 2330. Fig. 196. Portions of three successive elements from the metaxylem of the female cone axis. The earliest element is to the left, the latest to the right. × 666. Fig. 197. Sectional view of the wall of the element shown in Fig. 193. × 2330. In Figs. 195 and 197, blackened areas are unlignified, stippled areas are lignified. Figs. 198-201, 204-208. Portions of tracheary elements from the stem (198-200, 204-208) and leaf (201) of *Ephedra* sp. In Fig. 198, 199, and 201, blackened areas are lignified, clear areas within the thickenings are unlignified. Blackened areas within pits in Figs. 200 and 206 represent tori. Figs. 198-200, 204-208. × 666. Figs. 201, × 1670. Figs. 202, 203. Portions of tracheary elements from the female strobilus of *Ephedra foliata*. × 666.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FIGS. 209-226.

Elements which possess a single, simple helix are common. Diagrammatic representations of the singly-doubly helical element may also be found (Fig. 207). Heterogeneity among the thickenings of the early elements is usually not pronounced, but this feature was found well expressed in the axis of the female strobilus of *E. foliata* (Fig. 203). Bordered pits appear in the early protoxylem elements (Figs. 199, 202) and in succeeding elements (Figs. 200, 201, 204, 206).

Later helical elements become progressively more reticulate in the sequence. There are generally a considerable number of forks and anastomoses associated with the pit trusses (Fig. 200) or pore trusses (Fig. 208) and if the pits are close together vertically, the element is more reticulate than helical. Reticulate elements such as the one illustrated in Fig. 204 are not common in the stem and their transition from clearly recognizable helical elements tends to be rather abrupt. In the leaf, on the other hand, reticulate elements are common (Fig. 201).

Centripetal wall filling can be seen toward the end of the sequence of cell types in the metaxylem (Fig. 206). *Tangential wall filling* in the sequencial sense occurs.

Certain of the larger pits in the helical and later elements lose their pit closing membranes and become pores (Fig. 208) as is well known (*see* Bailey, 1944). In *Ephedra* the pores tend to develop in uniseriate longitudinal series in the protoxylem, but uniseriate arrangement is usually lost in the late metaxylem and into the secondary xylem where the pores tend to be in compact groups. The simple perforation is thought not to exist in *Ephedra*, but one was observed in the secondary xylem. The perforation plate was actually simple on one side only, and was matched with a group of four pores in the opposing wall of the next vessel member in the vertical series.

The primary wall of tracheary elements of *Ephedra* tends to be unlignified throughout the primary xylem and the secondary wall for the most part lignified. Occasionally, however, one will see in a face view of an element unlignified areas in the secondary system (Figs. 198, 199, 201, 205, clear areas). These were seen occasionally in *E. antisyphilitica* and commonly in *E.* sp. On stretching of the early protoxylem elements, the thickenings often rupture across these unlignified areas (Figs. 198, 199, 205). The unlignified areas could be seen in protoxylem elements rather close to the shoot tip and therefore seem to represent areas where lignin was never added to the cellulose framework rather than areas where lignin had been digested away later.

GNETACEAE — Simple annular elements appear first in the protoxylem sequence of *Gnetum* (Fig. 209). These are followed by annular-helical hybrid types of elements and then by helical elements. The helical elements are single, double or singly-doubly (Figs. 209-212). The primary wall of the early elements of *Gnetum* is thin and unlignified. This characteristic is usually present throughout the primary xylem and into the secondary xylem. An unusual exception to this generalization is shown in Fig. 219 which shows a slightly thickened and lignified base wall. Bordered pits appear relatively early in the protoxylem (Fig. 209) and are present in all subsequent elements in the sequence (Figs. 209-212, 214, 215-219). The pits are generally vestured as the result of the presence of small outgrowths around the pit apertures (Figs. 210, 214, 215, 218). The pit truss in the early elements (Fig. 209) tends to be a group of secondary thickenings, but in

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FIGS. 209-226 — Figs. 209-218. Portions of tracheary elements from the stem of *Gnetum gnemon*. Structures in Figs. 209, 210, 215, 216, and 218 are bordered pits while the one in Fig. 211, those in Fig. 213, the five larger ones in Fig. 214, and the two larger ones in Fig. 217 are pores. Fig. 219. Portion of a tracheary element from the stem of *Gnetum leyboldii*. Figs. 220-226. Portions of tracheary elements from the axis of the female strobilus of *Welwitschia*. Sectional views of double walls in Figs. 222, 223. Note the four pits in Fig. 223. The structures in Figs. 221, 224, and 226 are pits, while in Fig. 225 the three upper ones are pits and the three lower (larger) ones are pores. All × 666.


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FIGS. 227-245.

later elements the number of secondary thickenings supporting the bordered pit become reduced progressively until in the later protoxylem and early metaxylem the secondary wall around the pits is in the form of a sheet (Fig. 218). In other words, tangential wall filling takes place in the vicinity of the pits more than elsewhere. Eventually, toward the end of the metaxylem, tangential wall filling is complete (Fig. 214). The helical pattern often seems to be preserved in the sequence of cell types until the wall is almost completely tangentially filled. Only occasionally does one see what can be clearly referred to as a reticulate element (Fig. 219).

As in *Ephedra*, certain pits are larger and lose their pit closing membranes to become pores (Figs. 211, 213, 214, 217). In the protoxylem the pores are in uniseriate order near the ends of the cells (Fig. 213) as in *Ephedra*. In the metaxylem the pores are larger and are in closer proximity to each other (Fig. 214).

WELWITSCHIACEAE — The early protoxylem elements of *Welwitschia* are either singly helical or singly-doubly helical (Figs. 220, 224). The base wall (presumed primary walls in the early elements) tends to be slightly thickened in the early elements of the sequence and more and more thickened in the later elements (Figs. 222, 223). In sections of mature organs (stems, roots, inflorescence axes, and strobilar axes) all of the cell wall layers are usually seen to be strongly lignified. Sectional views of the helical thickenings show unusual and irregular shapes (Figs. 222, 223).

Bordered pits which are often vestured as in *Gnetum* appear in the relatively early protoxylem and in subsequent elements (Figs. 221, 224-229). Some of these structures develop into pores as in *Ephedra* and *Gnetum*. In the early elements of *Welwitschia* rows of pores are uncommon. The single pore is by far of the most common occurrence (Figs. 228, 232, 241), two pores at the same end of an element are less frequent (Figs. 229, 240), and three pores have been seen only once (Fig. 225). Only singly occurring pores have been seen in last formed metaxylem and "secondary" xylem. Previous reports indicate that only the single pore exists in *Welwitschia*.

The helical pattern of the protoxylem gives way in the sequence to a reticulate one as numerous forks and anastomoses appear (Figs. 225-228). In addition, the openings of the reticulum become narrower and narrower as the result of well expressed tangential wall filling (Figs. 226-229).

Centripetal wall filling is similarly well expressed in *Welwitschia*. The base wall, which is a presumed primary wall in the earliest members of the sequence, is seen to be progressively thicker in later and later formed elements and therefore the more internal thickenings, which are

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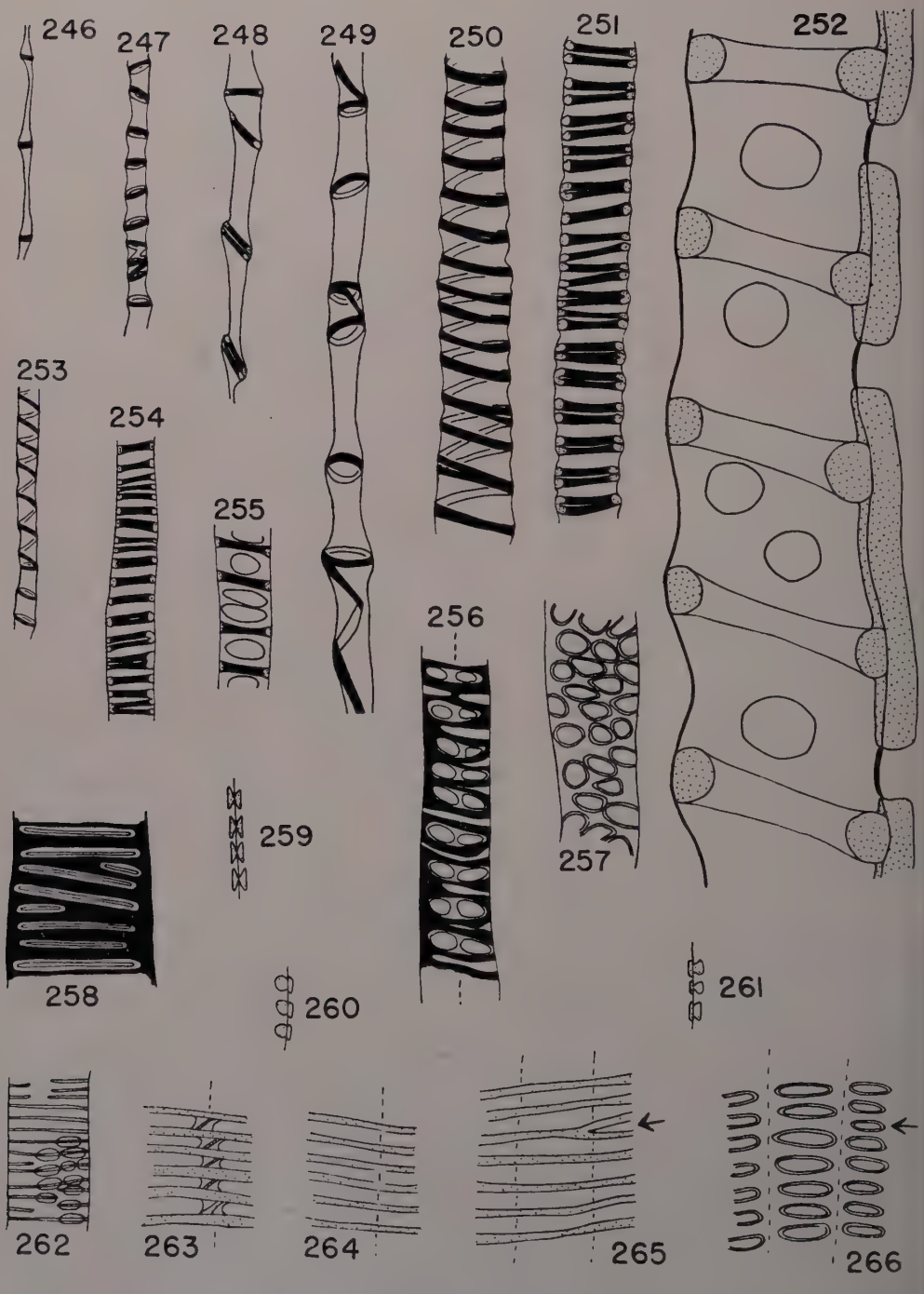
FIGS. 227-245 — *Welwitschia*. Figs. 227-229, 235, 242. Portions of face views of tracheary elements. In Fig. 228, one pore is shown; in Fig. 229, two pores are shown. Fig. 230. Sectional view of the walls of two adjacent tracheary elements. The cell to the left is a pitted element; the one to the right is a reticulate element. Fig. 231. Same as Fig. 230, but different cells. Fig. 232. Sectional view of the end walls of two reticulate vessel elements in a series. One pore is shown. Fig. 233. Sectional view of the wall of a tracheary element. None of the indentations or grooves in the walls here are lateral extensions of elongate inner pit apertures. Fig. 234. Same as Fig. 233, but essentially all of the indentations or grooves here are the lateral extensions of elongate inner pit apertures. Fig. 236. Sectional view of the same cell in Fig. 235. Fig. 237. Sectional view of the adjacent walls of two pitted elements. Fig. 238. Sectional view of the ends of two overlapping pitted elements. Fig. 239. Sectional view of the adjacent walls of two pitted elements showing a pit pair with several apertures. Fig. 240. Sectional view of the end walls of two vessel elements in a series. Two pores and three pits are shown. Fig. 241. Same as Fig. 240, but reticulate elements and one pore shown. Fig. 243. The same pit shown in Fig. 242, but at a lower focal plane, showing that the slit-like opening to the right of the pit in Fig. 242 is in reality the edge of the inner pit aperture. Fig. 244. Bordered pits with multiple apertures in face view. Inner apertures shown by solid lines, outter apertures by dotted lines. Fig. 245. Sectional view of the wall of the same cell shown in Fig. 244 and the opposing wall. Figs. 227-243 from the major axis of the male inflorescence. Figs. 244, 245 from the root. All × 666.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FIGS. 246-266.

helical in the earlier members of the sequence and reticulate in the later ones, become relatively less and less pronounced until the inner surface of the cell is essentially smooth. The entire sequence with respect to centripetal wall filling is shown by Figs. 222, 223, 230 (right side), 231 (right side), 232, 233, 241, 236, and 238. The walls of the tracheary elements of *Welwitschia* are often so thick and densely staining that irregularities on the inner wall are not seen in surface view unless they are of considerable magnitude, e.g. Fig. 235 is a representation of the surface view of the same element shown in sectional view in Fig. 236.

The inner pit apertures of late formed tracheary elements of *Welwitschia* are very narrow and elongate, and oriented nearly transversely to the axis of the cell. The elongate inner aperture is often not situated symmetrically, but may extend for a greater distance toward one side or another. The inner apertures at a given focal plane may occasionally appear in face view to be a part of the cell's inner reticulum, e.g. the slit to the right of the pit in Fig. 242 at another focal plane appeared as in Fig. 243. In sectional view the edges of elongate inner apertures if viewed at a focal plane which does not include the pit chamber will appear to be irregularities on the inner surface of the wall. As far as could be determined, all of the apparent irregularities on the inner surface of the wall shown in Fig. 234 and some of those in Fig. 236 are the edges of elongate inner pit apertures.

Pits in *Welwitschia* often show multiple apertures. In the series of pits shown in Fig. 244 in face view and in a similar series from another part of the same cell in Fig. 245 in sectional view, multiple apertures are shown. In Fig. 244, inner apertures are shown with solid lines while outer apertures are shown with dotted lines. In each of these pits, there is one major pit canal and one to several minor ones. The pit pair shown in Fig. 239 (fourth from the bottom) had two major pit canals in either member of the pair.

The early elements of the three "Gnetalean" genera are referred to rather briefly in previous literature. Pearson (1929) describes *Ephedra* as having "normal gymnospermous structure, *Gnetum* as having elements with spiral, annular and reticulate thickenings among which bordered pits occur at intervals and *Welwitschia* as having annular, spiral and reticulate elements and in addition elements in which all three kinds of thickening are combined. Bailey (1925) described the occurrence of circular bordered pits in early formed elements of *Ephedra*.

The simple perforation plates which occur commonly in *Gnetum* and *Welwitschia* and which have been seen only once in *Ephedra* have been interpreted (Bailey, 1944) as being derived by the "fusion" of several smaller ones. The evidence in support of this interpretation comes primarily from *Gnetum*, where in the primary xylem perforation plates are at first composed of a linear series of pores,

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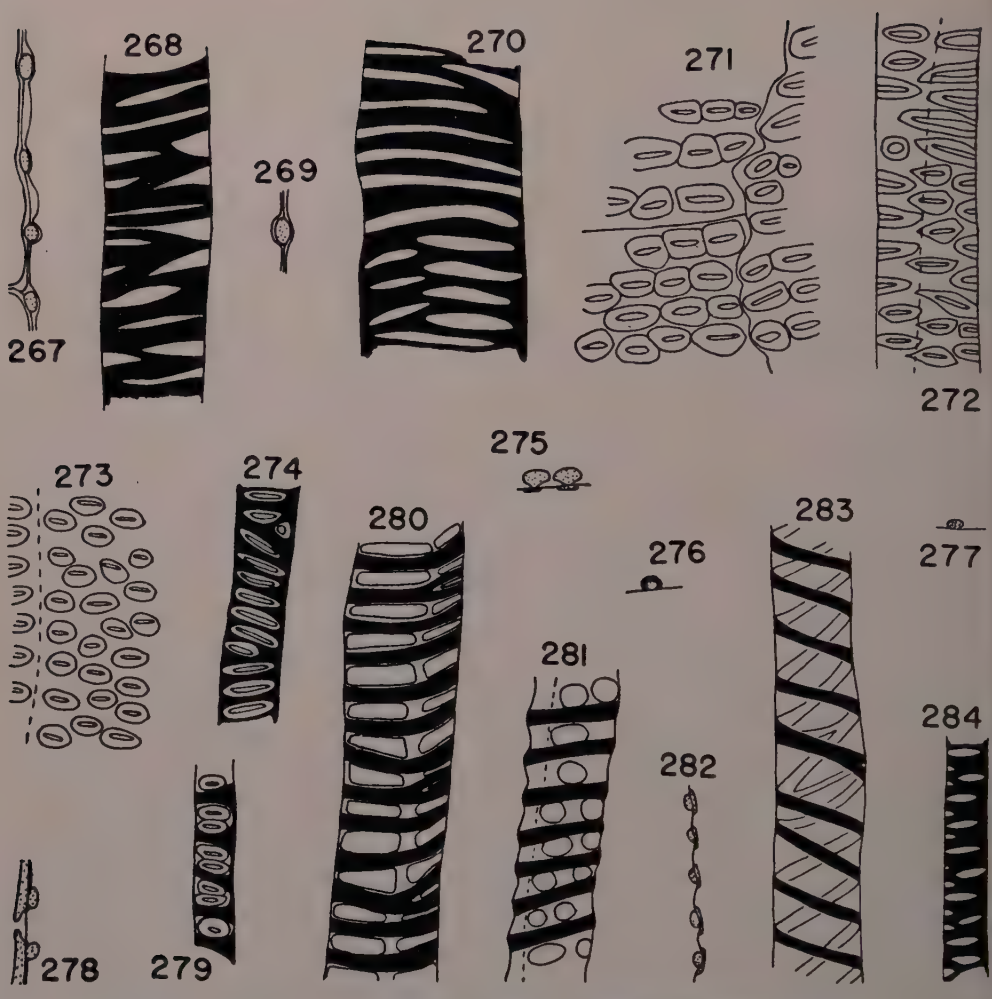
FIGS. 246-266 — Figs. 246-251. Portions of tracheary elements from the stem of *Hedera helix*. × 666. Fig. 252. Portion of a protoxylem element and wall of an adjacent parenchyma cell from the stem of *Michelia fuscata*. × 4440. Figs. 253-257. Portions of tracheary elements from the stem of *Ligustrum vulgare*. × 666. Fig. 258. Portion of a metaxylem element from the stem of *Liriodendron tulipifera*. × 666. Fig. 259. Sectional view of the walls of two adjacent metaxylem elements from the stem of *Magnolia grandiflora*. × 666. Fig. 260. Sectional view of the wall of the same cell shown in Figs. 263 and 264 and the wall of the adjacent parenchyma cell (on right). × 666. Fig. 261. Sectional view of the wall of the same cell shown in Figs. 265 and 266 and the wall of an adjacent parenchyma cell (on left). × 666. Fig. 262. Face view of a portion of a metaxylem element from the stem of *Casuarina equisetifolia* and the outlines of the simple pit pairs shared with overlying parenchyma. Only the slit-like apertures of the tracheary element are shown, the borders which are very broad are omitted for simplicity. × 666. Fig. 263. Outter focal plane of the face view of an early metaxylem element from the stem of *Magnolia grandiflora*. × 666. Fig. 264. Inner focal plane of the same portion of the same cell shown in Fig. 263. × 663. Fig. 265. Inner focal plane of the face view of a metaxylem element from the stem of *Magnolia grandiflora*. × 666. Fig. 266. Outer focal plane of the same portion of the same cell shown in Fig. 265. Arrows indicate points of correspondence.



FIGS. 267-284 — Figs. 267-271. From the stem of *Citrullus vulgaris*. Fig. 267. Sectional view of the wall of a helical element (right) and the opposing walls of parenchyma (left). Stippled wall is lignified, clear wall is unlignified. Fig. 268. Portion of a tracheary element. Fig. 269. Sectional view of the wall of the same cell shown in Fig. 270, and the wall of an adjacent parenchyma cell (on right). Lignified wall is stippled. Fig. 270. Portion of a tracheary element. Fig. 271. Portion of a pitted element showing (sinuous line) an edge of the vessel element which corresponds to the intersection of the parenchyma cell walls, the plane of which is at right angles to that of the drawing. Figs. 272, 273. Portions of tracheary elements from the stem of *Hisbiscus esculentus*. Broken line indicates a cell edge. Figs. 274-284. From the stem of *Cordyline* sp. Fig. 274. Portion of a metaxylem element. Fig. 275. Sectional view of the wall of a metaxylem element (top) and the opposing wall of a parenchyma cell (bottom). Fig. 276. Sectional view of a part of the wall of a helical element. Fig. 277. Sectional view of a portion of the wall of a reticulate element. Fig. 278. Sectional view of the wall of a pitted element (left) and a helical element (right) showing a half-bordered pit pair. Fig. 279. Face view of the same double wall shown in Fig. 278. Figs. 280, 281. Portions of protoxylem elements. Broken line represents a cell edge. Fig. 282. Sectional view of the wall of a helical element (left) and the opposing wall of a parenchyma cell (right). Figs. 283, 284. Portions of tracheary elements. All × 666.

then a transition to grouped pores which are closer and closer in proximity to each other, then grouped pores showing various stages of " fusion " which persist along with the large simple perforation well into the secondary xylem. A similar sequence

rarely showing complete fusion is to be found in *Ephedra*. The "fusion" interpretation is therefore well supported in *Gnetum* and in *Ephedra*. In *Welwitschia*, however, one finds in the early primary xylem mostly vessel members with relatively large simple perforations, occasional vessel members with two pores, and rarely with three. No evidence of fusion of adjacent pores has been found, and where the pores are in twos or threes, they are always linearly arranged. The hypothesis that a number of smaller pores phylogenetically fused to form a larger one seems quite unsupported in *Welwitschia*, but rather it is suggested that there has been a reduction in the number of pores and, therefore, the single pore which is usually to be found on the end plate of the vessel member of *Welwitschia* more likely is the homolog of one of the individual pores of the Ephedroid type of multiple perforation plate and represents a phylogenetically transformed single bordered pit.

Angiosperms — The size of the sample of flowering plants used in this study permits few generalizations as to their primary tracheary element structure. This is similarly true even if this sample is added to all those which have been previously described. From the point of view of the present study, the mere presence of certain structural features is of some importance. Little or nothing can be said with certainty concerning the absence of certain features in the angiosperms as a whole, obviously.

In terms of the very little information presently at hand, the angiosperms may possess the simplest and most diagrammatic structural types of early protoxylem elements. The simplest type of protoxylem element to conceive is the one in which there is a thin primary wall and no secondary wall as has been described from the embryo of *Gleditsia* (List, 1958) where it exists only for a very short time. This type of protoxylem element may be of more widespread occurrence, but to date has not been observed elsewhere. The simple annular element with distinct, unelaborated rings is probably widespread among angiosperms (Figs. 246, 247). It has been described and illustrated in essentially every textbook of General Botany and Plant Anatomy published in the past 150 years. It was not well known until the work of Von Mohl (1839).

Some variations do occur among the annular elements of the angiosperms. The full extent of the range in variation will be known only after a very careful study of many hundreds of angiosperms. Forked rings, or directly attached rings, occur apparently sporadically. It is not known whether or not there are any angiosperms which possess extensive series of forked rings. Pairs of rings with simple indirect connections similarly occur; these are illustrated in Figs. 247 and 249 from *Hedera*. Rings in which there is an internal groove have been seen in *Hedera* (Fig. 248). Here and there the groove is deep enough to produce some doubling. Annular-helical hybrid types of elements are of course well known (Figs. 253, 249).

The simple helical elements have been known in angiosperms since the observations of Grew (1682) and Malpighi (1675) and have been illustrated and described many times. The double helical elements are similarly well known. The apparently multiple helical elements mentioned by de Bary (1877) and Skutch (1927) as occurring in *Musa* and probably also those described by Treviranus (1806) from *Amomium* with occasionally more than a dozen parallel helical thickenings are not of a simple structure. Adjacent thickenings in the groups of parallel ones are interconnected by fine strands of secondary wall material. This has also been observed in *Pandanus*.

The helix may be internally grooved as another variation. This was illustrated by Brisseau-Mirbel (1815) and Esau (1953). The groove occasionally is deep enough here and there to result in doubleness of the thickening (Figs. 250, 251, 254).

Branched helical thickenings are apparently not uncommon among angiosperms (Figs. 250, 283). The singly-doubly (to multiple) type of helical element so diagrammatically represented in *Ephedra*, *Gnetum*, and *Welwitschia* has not been observed.

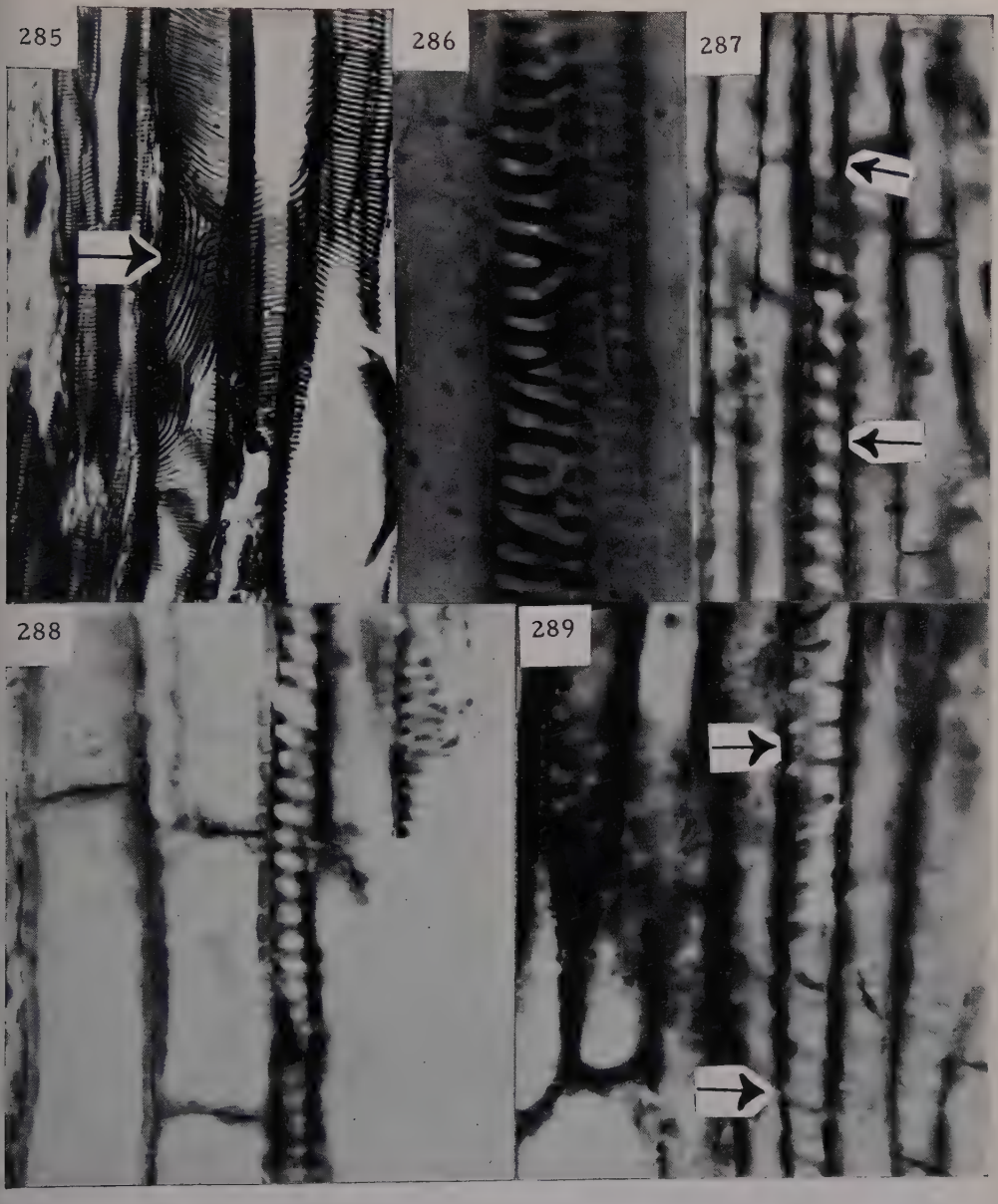
The reticulate element shows considerable variation among angiosperms. A

survey of various angiosperm groups in terms of details of structure of the reticulate elements found in the primary xylem should prove quite rewarding. Among dicots, reticulate elements in which the openings in the reticulum are transversely oriented and cross cell edges are common (Figs. 268, 270) [*see* also Esau (1953), Fig. 11.4; Eames & McDaniels (1947), Fig. 62; Jeffrey (1917), Fig. 13]. These elements often follow in the sequence of cells in the primary xylem other elements which are intermediate between helical and reticulate in that they possess obvious helical organization, but in addition anastomoses between adjacent gyres. Reticulate elements in which the openings are more or less of circular form but with slight borders (Fig. 257) occur; the extent to which this type of element occurs among angiosperms is not known. Irregular reticulate elements in which the openings are circular to elongate to irregular and oriented from transversely to vertically all within the same cell are known. See the illustrations of Cheadle (1943) Fig. 8 and Esau (1953) Fig. 11.5. A survey of angiosperm primary xylem may show the irregular reticulate element to be more or less characteristic of certain monocot families. In certain monocots, e.g. *Zebrina*, *Cyperus*, a type of reticulate element occurs in which the openings are large, rectangular, and somewhat elongate transversely, and are uniformly trans-edge opposite. It is possible that a survey will show that this type of reticulate element also is of restricted distribution. Occasionally openings in reticulate elements develop rather extensive borders (Fig. 272). Note that this element from the stem of *Hibiscus* shows openings crossing cell edges.

Angiosperm pitted elements have been described in possibly hundreds of publications. It is desirable to point out several features of the elements of certain genera here in order to arrive at a generalized concept. Pitted elements, either transitionally pitted or circular pitted, generally show some rowed arrangement on the faces. The rows may be either transverse or slanted (Figs. 271, 273). The rows are often disturbed suggesting a branching of the structural organization of the wall (Fig. 271). This is considered comparable to those points where, in the scalariformly pitted elements, a given elongate pit ends within a face and is not situated opposite another (Figs. 258, 274). The pits, in addition, in those few angiosperms in which this characteristic has been observed, are trans-edge opposite (Figs. 273, 271), that is, the rows may be seen to continue on adjacent faces.

The primary cell wall in angiospermous primary xylem tracheary elements is often thin and unlignified (Fig. 277) as is stated in essentially every textbook of plant anatomy. It may also be to a large extent lignified as in many of the elements of *Cordyline*, or the secondary wall may show a lignified core and an unlignified inner portion (Fig. 276).

A secondary-secondary cell wall of the type observed in the Psilotaceae and in the Cycadaceae is quite pronounced in certain Angiosperms. It has been seen in *Magnolia*, *Liriodendron*, *Michelia*, *Citrullus*, and *Cordyline*. In the three Magnoliaceous genera it was most distinct. It was present only between the secondary thickenings (Figs. 252, 278, 279) in all, but *Citrullus* where it also covered the secondary thickenings (Figs. 267, 269). Pits were frequently found in the opposing walls of elements adjacent to early primary xylem elements. Figure 252 (*see* also Figs. 287-289) shows such pits in face view and also in sectional view where it can be seen that the secondary-secondary wall of the helical element outlined the matching pits to those in the adjacent parenchyma cells. The pits seen in face view in Figs. 255, 256, 280 and 281 and in sectional view in Figs. 275 and 282 may be unmatched pits in that the walls of the tracheary elements were so thin that the counterpart pits could not be detected. It will be noted that the simple pits in the parenchymatous elements (lower side in Fig. 275, and right side in Fig. 282) are in these cases smaller in diameter than the width of the " border " on the opposite side. Pits observed between the secondary thickenings of primary xylem elements were never seen to cross cell edges. Figure 262 illustrates a condition from the metaxylem of *Casuarina* comparable to those described above. Here is shown a face view of a



FIGS. 285-289 — Fig. 285. Metaxylem elements from the stem of *Dennstaedtia*. Arrow indicates crossing elongate pits. × 100. Fig. 286. A protoxylem element from the stem of *Psilotum nudum* showing a major helical thickening and a secondary-secondary wall outlining simple pit-like structures. × 450. Fig. 287. A helical element from the stem of *Michelia fuscata* showing pits in the tracheary wall between the gyres. × 450. Fig. 288. Section through the protoxylem of the stem of *Liriodendron tulipifera* showing pit pairs in sectional view between parenchyma cells and a helical element. × 450. Fig. 289. As Fig. 287, but *Liriodendron tulipifera*. × 450.

double wall on which can be seen the apertures of elongate bordered pits and the superimposed pattern of simple pits of an adjacent parenchyma cell. The widths of the simple pits were nearly, but slightly less than, the same as the widths of the borders of the pits of the tracheary element.

Koernicke (1925) illustrated and described stretched spiral elements of *Polygonum* in which the spiral thickening had pulled away from the rest of the wall. He noted that where the narrow base of the thickening had been attached there was a distinct groove left in the remaining wall. The grooved wall was shown to be of significant thickness as was also a layer outside of this which he presumably considered to be intercellular substance (*see* his Fig. 1). The structural parallel between Koernicke's illustration and the helical element of *Michelia* (Fig. 252) suggests that probably the grooved wall in *Polygonum* was the secondary-secondary wall deposited over the previous wall after the helical thickenings were established.

A structural framework in pitted angiospermous tracheary elements upon which the pits are superimposed can be detected occasionally. This is illustrated in the early and intermediate metaxylem of *Magnolia*. Some of the early metaxylem elements (Fig. 263) show at a focal plane at the outer limit of the wall nearly transversely oriented helical thickenings with a small sheet of extra wall material between each pair of adjacent bars along the edges of the cell. The dotted line in the drawing represents the cell edge. At a focal plane deeper in the cell the thin sheets between the bars disappear (Fig. 264). A very similar situation has been described and illustrated by Warburg (1883) in *Caulotretus* (*see* his Fig. 7). A similar condition is illustrated from the later metaxylem where the wall material between the helical thickenings was more extensive and pits were clear. The details of matching of these pit areas are shown in Figs. 260 and 261 where it can be seen that the simple pits of the adjacent parenchymatous elements are narrower than the opposing opening of the tracheary element. Commonly one observes in pitted elements of angiosperms a coarse irregular to helical thickening on the inside of the wall of a much greater order of magnitude than the so-called " tertiary spirals ". For example, this is readily observed in vessels of various species of *Quercus*. It is not unlikely that at least some such thickenings are indicative of an ancestral wall pattern upon which the pits have been imposed.

Discussion

The terms used today to describe the various types of tracheary elements, i.e. annular, helical, reticulate, scalariform, pitted, etc., are all words of ancient vintage, dating back at least a century and a half and some longer. They have been used by some authors strictly as adjectives and by others as " technical terms ". When used as technical terms ideally they should be stictly defined as closely as possible and be as unambiguous as possible, and if they are of adjectival origin then they should also be in some way descriptive. When used merely as adjectives, they should be used in a manner which conforms to accepted dictionary meanings. The terms under present consideration appeared first in the botanical literature as merely adjectives and gradually and *incompletely* evolved into " technical terms ". Today they are used mostly as technical terms; previous to the middle of the last century they were used commonly as mere adjectives. In many instances it is quite impossible to determine precisely in which of the two general ways a given author is using certain terms. If one reviews the various applications of these terms and similar ones, he is struck by the extremely variable way in which they have been applied resting on, in some cases, incomplete or erroneous observations or faulty interpretations. From the following table it will be noticed that the term " spiral " was frequently applied to the annular element before 1850. This followed the misinterpretation of Link (1843) that the annular element was derived ontogenetically from a spiral element, an idea which has appeared again recently (Engard, 1944). Unstretched simple reticulate elements have frequently been referred to as " spiral " either as an inter-

pretation or a misobservation. Among relatively recent workers there seems to be little agreement as to the range of elements included under "reticulate", "pitted", or "scalariform".

The term "scalariform" is of particular interest because of its history and variable current usage. This term before the turn of the century was used almost exclusively to refer to what is often called today the "scalariformly pitted element". Before the middle of the 19th century it was generally considered to be a specific term under a broader or generic term, "Leiterförmig". The presumed synonyms of leiterförmig were "leisterförmig", "rayé", and "fendu". The German "treppenförmig" was an exact synonym of "scalariform". The generic term "leiterförmig" (and its three synonyms) was used to refer to a wide variety of tracheary elements which in side view presented a ridged, barred, rayed, or ladder-like appearance; in other words, to unstretched annular elements, unstretched simple helical elements, helical elements with forks, helical elements with forks and anastomoses, reticulate elements with transversely elongate openings, and scalariformly bordered pitted elements. As far as could be determined, the generic terms "leiterförmig", "rayé", and "fendu" had no English counterpart and were never accurately translated. The terms "leiterförmig" and "treppenförmig" have nearly identical English literal translations. It is assumed that this is the source of the usage of "scalariform" in the English literature to refer not only to scalariformly bordered pitted elements, but also to various other types of elements of the protoxylem and metaxylem with some sort of barred appearance in side view. There are some exceptions to the general pattern of usage. Rudolphi (1807) referred to slightly elaborated helical elements as "treppengänge". This usage fits the adjectival meaning of the word, but not necessarily the technical meaning which was current at his time. The term "leiterförmig" in more modern German literature (*see* Table below) is used in the specific sense of the original "treppenförmig" or "scalariform" to refer to the scalariformly bordered pitted element. In the modern English literature the only unambiguous usages of the term "scalariform" are in the expressions "scalariform-reticulate" and "scalariformly pitted" and certainly, in the interest of accurate terminology, all other usages should be avoided.

TABLE 1*

The Annular Element	Element with ring bands, ring thickenings or annular thickenings; ringförmig Gefäss; Ring Gefäss; Ringgefäss; ring vessel; cellula annulifera; vasa annularia; vasseau annulaire; vaisseau annelée; annular element; annular vessel; Ringtracheid; Ringfasserzelle.	Baillon, 1882, 1883; Barkley, 1927; Bischoff 1833; Boodle, 1901; DeBary, 1877; DeCandolle 1821; Eames & MacDaniels 1947; Esau, 1953; Fry, 1954; Foster, 1947; Gustin & Sloover, 1955; Gunkel & Wetmore, 1946; Holman & Robbins, 1934; Haberlandt, 1924; Hayward, 1938; Hartig, 1878; Intern. Assoc. Wood Anat., 1933; LeClerq, 1930; Luerssen, 1881; Link, 1843; Molisch, 1920; Molisch & Höfler, 1954; Ogura, 1938; Pratt, 1917; Rudolphi, 1807; Russow, 1872; Schleiden, 1844, 1849; St. Pierre, 1870; Scherer, 1904; Scott, 1949; Stover, 1951; Strasburger et al., 1908; Tschirch, 1889; Wiesner, 1898; Weis, 1878; Zimmermann, 1930, 1959.

*A summary of the terminology used to describe types of tracheary elements. The terms in the left-hand column are those used in the present study. The ones in the middle column are those which have been applied in the past. They are listed in synonymous groups, except for a few miscellaneous categories. Allowances must be made for the facts that in the earlier literature no distinction was made between tracheids and vessel members, that often the individual cellular components in a vertical series were not recognized, and that in some instances an author was not aware of the existence of a primary wall and thought only of the thickening bands.

TABLE 1 — *contd.*

	Falsche spiral Gefäss, fausse-trachée	Brisseau-Mirbel, 1815; Treviranus, 1806.
	Vaisseau fendu	Brisseau-Mirbel, 1815.
	Ringgerfäss or vasa annularia as a sub-type under Spiralgefäss or Spiroid.	Unger, 1846, 1866.
	Trachée spireau, vaisseau spireau	Slack, 1834.
	Ringförmig Spiralgefäss, vasa spiralia annularia, vasseau spiraux annulaire.	Bischoff, 1833.
	Vaisseau rayé	Bischoff, 1833
The Helical Element (Simple type)	Spirally thickened element; spiral element; element with spiral bands; Spiralgefäss; Spiral Gefäss; spiral tracheid; spiral vessel; cellula spirifera; trachée ou vaisseau spireau; vasa spiralia; vasseau spiraux; vasseau spiralée; Spiralfasserzell; spiral tube.	Atkinson, 1894; Baillon, 1882, 1883; Barkley, 1927; Bischoff, 1833; Bower, 1923; Boodle, 1901; Booth, 1933; Buchholz, 1933; Chrysler, 1937; Crafts, 1943; DeCandolle, 1821; Demalsy, 1953; De Bary 1877; Eames & MacDaniels, 1947; Esau, 1953; Ford, 1902; Foster, 1947; Fry, 1954; Gustin & Sloover, 1955; Hartig, 1878; Holman & Robbins, 1934; Hayward, 1938; Haberlandt, 1924; Int. Assoc. Wood Anat., 1933; Jeffrey, 1917; Luerssen, 1881; Link, 1843; Lestiboudois, 1840; LeClerq, 1930; McNicol, 1908; Meyen, 1830; Ogura, 1938; Penhallow, 1907; Pool, 1929; Pratt, 1917; Rudolphi, 1807; St. Pierre, 1870; Schleiden, 1844, 1849; Scott, 1949; Sifton, 1920; Slack, 1834; Stover, 1951; Strasburger et al., 1908; Treviranus, 1811; Tschirch, 1889; Unger, 1866; Von Mohl, 1839; Weiss, 1878; Wiesner, 1898; Zimmermann, 1930, 1959.
	Helical element, helicule.	Bischoff, 1833; Esau, 1953; Gunkel & Wetmore, 1946.
	Wahr Spiralgefäss	Bischoff, 1833; Treviranus, 1811.
	Trachée, trachea	Bischoff, 1833; Brisseau-Mirbel, 1815; Grew, 1682; Malpighi, 1675.
	Einfach Spiralgefäss, vasa spirilia simplicia	Bischoff, 1833; Unger, 1846.
	Schraubengefäss, Schraubengäng	Bischoff, 1833; Molisch, 1920; Molisch & Höfler, 1954; Russow, 1872; Scherer, 1904; Strasburger, 1891; Unger, 1866; Weiss, 1878; Wiesner, 1898.
	Spiroid	Link, 1839; Schleiden, 1844; Weiss, 1878.
	Vasa adducentia spiralia, v. chymifera, v. hydrogera, vasseau elastique	Bischoff, 1833.
	Air vessel, vasa pneumatochymifera, v. pneumatophora.	Bischoff, 1833; Grew, 1682; Malpighi, 1675.
The Helical Element (with close spirals, some forks and few anastomoses)	Scalariform element, scalariform protoxylem cell, Treppentracheid, Treppengäng.	Barkley, 1927; Booth, 1933; Chrysler, 1937; Eames & MacDaniels, 1947; Esau, 1953; Foster, 1947; Hayward, 1938; Jeffrey, 1912; Rudolphi, 1807; Sifton, 1920; Zimmermann, 1930, 1959.
	Cellula retifera	Schleiden, 1849.
	Vasseau rayé	St. Pierre, 1870.

TABLE 1 — *contd.*

	Vaisseau annelé-reticulé	Baillon, 1883.
	Spiral element with reticulate ramifications	Pool, 1929.
	Spiralgefäss, spiroid	Lestiboudois, 1840; Link, 1843.
	Spiral-reticulate	Baillon, 1882.
	Spiral grades into reticulate	deBary, 1877.
	Element with complex spirals	Crafts, 1943.
	Netzgefäss	Tschirck, 1889.
The Simple Reticulate Element	Spirally thickened element; spiral tracheid, spiral vessel, Spiralgefäss.	Faull, 1901; Ford, 1902; Lange, 1891; McNicol, 1908.
	Reticulate tracheid, cellula retifera	Atkinson, 1894; Schleiden, 1849.
	Treppengäng, finely scalariform element, protoxylem scalariform element, scalariform element.	Boodle, 1901; Eames & MacDaniels, 1947; Esau, 1953; Gwynne-Vaughan, 1901; Hayward, 1938; Rudolphi, 1807; Sifton, 1920.
	Netzformig Spiralgefäss or vasa reticulata as a sub-heading under Spiralgefäss.	Unger, 1846, 1866.
	Treppenförmige Zelle (which on stretching have appearance of netted cells).	Warburg, 1883.
The Reticulate Element (Metaxylem type, includes irregular to scalariform-reticulate)	Netzgefäss, cellula retifera, netzförmig Gefäss, vasa reticularia, vaisseau reticulaire, vaisseau reticulé, Netztracheid, reticulate element, Netzfasserzelle.	Baillon, 1882; Bischoff, 1833; Booth, 1933; Bower, 1923; DeBary, 1877; Eames & MacDaniels 1947; Esau, 1953; Foster, 1947; Heberlandt, 1924; Hartig, 1878; Hayward, 1938; Jeffrey, 1917; Lange, 1891; Link, 1842, Luerssen, 1881; Molisch, 1920, Molisch & Höfler, 1954; Pool, 1929; Pratt, 1917; St. Pierre, 1870; Schleiden, 1849; Scott, 1949; Stevens, 1911; Stover, 1951; Strasburger, 1908; Von Mohl, 1842; Zimmermann, 1930.
	Spiral Gefäss, Spiroid	Link, 1839; 1843.
	Falsch Spiralgefäss, fausse-trachée, falsch luftgefäss, vasseau spiraux faux, vasa spiralia spuria.	Bischoff, 1833; Brisseau-Mirbel, 1815; Slack, 1834; Triviranus, 1806.
	Netzförmig Spiralgefäss, vasa spiralia reticularia, vasseau spiraux ramifié et reticulé, or vasa reticulata as subheading under spiral Gefäss.	Bischoff, 1833; Unger, 1846, 1866.
	Vasseau rayé	Slack, 1834.
	Pitted element	Holman & Robbins, 1927, 1934; Lestiboudois, 1840.
	Irregular netted or pitted element	Cheadle, 1953.
The Scalariformreticulate Element	Vasseau rayé	Baillon, 1882; Slack, 1834.
	Treppengefäss, Treppengang, vasa calariformia, vasseau scalairé, scalariform element.	Bischoff, 1833; DeBary, 1877; Holman & Robbins, 1927, 1934; Smith & Kersten, 1942.
	Tube fendu	Bischoff, 1833.
	Leiter-oder leisterförmig verdicktes Gefäss, Leitergefäss.	Tschirch, 1889.
	Scalariform-reticulate element	Bailey, 1949; Chrysler, 1937; Eames & MacDaniels, 1925, 1947; Esau, 1953.
	Pitted element	Lestiboidois, 1840.

TABLE 1 — *contd.*

The Scalariformly Pitted Element	Spiralgefäss	Link, 1841.
	Treppengang, Leitergefäss, or vasa scalariformia as a sub-heading under Spiralgefäss.	Unger, 1846, 1866.
	Scalariform tracheid, Treppentracheid, Treppengefäss, Treppengang, vasa scalaria, Treppenzelle.	Atkinson, 1894; Baillon, 1882; Boodle, 1901; Bower, 1923; Chrysler, 1937; DeCandolle, 1821; Faull, 1901; Ford, 1902; Gunkel & Wetmore, 1946; Gwynne-Vaughan, 1901; Hartig, 1878; Hofmeister, 1867; Jeffrey, 1917; Lange, 1891; Luerssen, 1881; Ogura, 1938; Rudolphi, 1807; Stover, 1951; Strasburger, 1891; Tschirch, 1889; Von Mohl, 1842; Weiss, 1878.
	Leitergefäss, Leiterförmig Gefäss	Baecker, 1922; Haberlandt, 1924; Luerssen, 1881; Molisch, 1920; Molisch & Höfler, 1954; Russow, 1872.
	Scalariform cell is a loose descriptive term and may refer to a scalariform pitted tracheid.	Eames & MacDaniels, 1947.
	Scalariformly pitted element, scalariform pitted element, Leiterförmig getüpfelt tracheid.	Eames & MacDaniels, 1947; Esau, 1953; Ogura, 1938.
	Vaisseau fendu ou fausse-trachée	Brisseau-Mirbel, 1815.
	Netzförmig Gefäss	Bischoff, 1833.
	Scalariform element as a sub-heading under vaisseau rayé.	St. Pierre, 1870.
	Element with scalariform pitting	In much of the very recent literature.
The Pitted Element (type with more or less circular borders)	Netzförmig Gefäss, vasseau reticulé	Bischoff, 1833; St. Pierre, 1870.
	Netförmig Spiralgefäss	Weiss, 1878.
	Fausse trachée	Slack, 1834.
	Porös spiral Gefäss, vasa porosa, getüpfelt Gefäss, vasa areolata, Tupfelgefäss, Porengefäss, all as subheading under spiral Gefäss.	Unger, 1846, 1866.
	Vaisseau ponctué, Tüpfeltgefäss, Porengefäss, Tupfelgefäss, pitted element, Getüpfelt Gefäss, Punctirt Gefäss, Vaisseau poreaux, Hoftüpfelttracheid.	Baillon, 1882, 1883; Booth, 1933; Brisseau-Mirbel, 1815; deBary, 1877; Eames & MacDaniels, 1947; Esau, 1953; Foster, 1947; Jeffrey, 1917; Lestiboudois, 1840; Link, 1843; Luerssen, 1881; Meyen, 1830; Molisch, 1920; Molisch & Höfler, 1954; Pratt, 1917; Schleiden, 1844; Scott, 1849; Slack, 1834; Stover, 1951; Strasburger, 1908; Treviranus, 1811; Weiss, 1878; Wiesner, 1898; Zimmermann, 1930, 1959.

In the descriptive portions of this manuscript certain terms have been proposed. In all instances the terms were as descriptive as possible, and old established unambiguous terms were given preference over new ones. New ones were proposed only where existing terms did not cover certain new information. The need for a classification of tracheary elements is well brought out by variable terminology in past and present usage, the great variability in the structure of tracheary

elements, and also by the fact that most of the published information on tracheary elements is relatively useless because of inadequate terminology. The following is a summary of recommended terminology to be used in describing certain tracheary elements:

TYPES OF TRACHEARY ELEMENTS — A CLASSIFICATION.

I. *Unthickened elements* (tracheary elements in which there is a primary wall and no secondary wall) (List, 1958).

II. *Annular elements* (tracheary elements in which there is a secondary wall in the form of rings).

A. *Simple annular elements* (annular elements in which the rings are unelaborated and distinct from each other) (Figs. 167, 209, 246).

B. *Directly attached annular elements* (annular elements in which adjacent rings are joined directly to each other) (Bierhorst, 1958; Figs. 8, 9).

C. *Indirectly attached annular elements* (annular elements in which adjacent rings are united by additional strands or sheets of secondary wall material) (Figs. 4, 49, 66, 68; Bierhorst, 1958, Fig. 32).

D. *Reticulated annular elements* (annular elements in which the rings are distinct, but each one is in the form of a reticulum) (Bierhorst, 1958, Figs. 2, 19, 20).

E. *Grooved annular element* (annular element in which the rings are grooved on their inner surfaces).

B-E. Intermediate form between *directly attached annular* and *grooved annular* (where the groove is deep enough to result in some complete doubleness of the rings here and there (Fig. 170).

III. *Helical or spiral elements* (tracheary elements in which the secondary wall is in the form of a helix).

A. *Singly helical element* (helical element in which the thickening is in the form of a single fibrous band).

B. *Doubly helical element* (helical element in which there are two parallel thickening bands).

C. *Multiple helical element* (helical element in which there are a number of parallel thickening bands) (Fig. 128).

D. *Variable multiple helical element* (helical element in which the thickening forks and recombines here and there so that the number of bands at given levels in the cell varies. 1-2 Variable helical element: one in which the variation is from one to two bands within the cell, etc.) (Figs. 126, 127, 172, 190, 191, 207, 212, 220).

E. *Reticulated helical element* (helical element in which the helical band itself has an internal reticulum).

F. *Compound helical element* (helical element in which a number of helical bands are joined to each other by interconnections of secondary wall material to form a single ribbon-form band).

G. *Grooved helical element* (helical element in which the thickenings are grooved on their inner surfaces) (Esau, 1953, Fig. 11.3E).

B-G. Intermediate form between *doubly helical* and *grooved helical* (Figs. 250, 251).

IIA-IIIA. *Annular-helical element* (element which is annular in part and helical in part) (Figs. 24, 26, 109, 117, 125, 138, 139, 169, 177, 199).

IV. *Reticulate elements* (tracheary elements in which the secondary wall is in the form of a network).

A. *Simple reticulate element* (reticulate element in which the network is made up of a system of fine strands; the openings are usually transversely oriented in the unstretched state and irregular to hexagonal in the stretched state) (Figs. 6, 7, 8, 120, 121, 140, 148).

B. *Scalariform-reticulate* (reticulate element in which the secondary wall is relatively massive and in which the openings are in the form of transversely elongate slits with pointed edges).

1. *Edge continuous scalariform-reticulate* (openings in the reticulum cross cell edges) (Figs. 60, 81, 268, 270).

2. *Edge discontinuous scalariform-reticulate* (openings in the reticulum do not cross cell edges).

a. *Trans-edge alternate scalariform-reticulate* (openings in the reti-

culum alternate with each other across cell edges) (Fig. 53).

b. *Trans-edge opposite scalariform-reticulate* (openings in the reticulum fall opposite each other across cell edges, i.e. transverse row of openings continued around a corner) (Fig. 154).

C. *Rectangular reticulate* (openings in reticulum rectahedral). (Only edge discontinuous, trans-edge opposite forms known) (Figs. 35, 36).

D. *Circular or eliptical reticulate* (openings in reticulum relatively large and rounded).

1. *Edge continuous circular or eliptical reticulate* (some of the openings in the reticulum cross cell edges) (Figs. 112, 257).

2. *Edge discontinuous circular or eliptical reticulate* (openings in the reticulum restricted to cell faces and do not cross cell edges; grades insensibly into circular bordered pitted type)

E. *Irregularly reticulate element* (openings in the reticulum of various shapes and orientations) (Cheadle, 1943, Fig. 8; Esau, 1953, Fig. 11.5D).

IIID-IVB 1. *Helical-reticulate* (helical element with forks and anastomoses in the thickening system, but still has a recognizable helical pattern; grades into edge continuous scalariform reticulate) (Figs. 73, 130, 141).

IIA-IVA or IIC-IVA. *Annular-reticulate* (element in which the secondary wall is in the form of a system of rings interconnected by a simple network of thickenings (Fig. 50, lower part; Fig. 69, in part; Fig. 118, in part; Fig. 119, in part).

V. *Pitted* (element in which the openings, either circular, elongate, or semi-elongate or lens-shaped have rounded edges except where crowded or lens-shaped and broad borders except where pits are minute).

A. *Scalariformly bordered pitted* (pits elongate or semi-elongate transversely, more or less).

1. *Trans-edge alternate scalariformly bordered pitted* (pits alternate across cell edges) (Figs. 15, 61).

2. *Trans-edge opposite scalariformly bordered pitted* (pits opposite across cell edges) (Figs. 143, 144, 159).

B. *Oblique and ob-scalariformly bordered pitted* (elongate pits oriented obliquely or vertically) (Figs. 65, 145, 146, 147, 285).

C. *Intra-face rowed pitted* (pits on a given face of the cell falling in rows).

1. *Transversely rowed pitted* (pits in transverse rows) (here are included the pitted elements with opposite and transitional pitting) (Fig. 271).

2. *Obliquely or vertically rowed pitted* (pits in oblique or vertical rows; here are included some of the alternate pitted elements). Under C 1 and C 2: (a) *Trans-edge opposite . . .* (rows of pits continued across cell edges).

(b) *Trans-edge alternate . . .* (rows of pits alternate across cell edges). Under C 1 and C 2: *Tilted axis transversely rowed pitted*, etc. (where the long axes of the pits do not lie along the long axes of the pit rows) (Fig. 155).

D. *Grouped pitted element* (pits on the faces in irregular cluster, sometimes surrounded by rim of Sanio).

E. *Irregularly pitted element* (pits on the faces not in apparent rows or clusters).

F. *Uniseriate bordered pitted* (elements with a single, vertical row of pits on a given face). Corresponds in part with V A1.

1. *Trans-edge alternate uniseriate bordered pitted* (pits alternate across cell edges) (Figs. 12, 13, 206).

2. *Trans-edge opposite . . .* (pits are opposite across cell edges).

The crossing of cell edges by openings in the secondary wall or their restriction to cell faces is certainly related to the establishment of edges and faces during the growth of the cell which is to give rise to a tracheary element. In a tissue in which the cell walls are elastic and in which the cells are enlarging differentially or in which cell divisions are still occurring, the edges and faces of the individual cells are not completely determined. If, for example, two cells A and B with completely elastic walls are situated side by side and separated by a common com-

pound middle lamella, and cell B divides in a plane such that the new cell wall is at right angles to the partition wall, then cell A will bulge out in the direction of cell B such that there will be a separate face in contact with each of the two daughter cells of B separated by a new cell edge. It is assumed that, in the protoxylem, cell edges and cell faces are not yet established at the time when the early tracheary elements determine their pattern of wall thickening and hence the openings do not conform to cell faces. In an annular element when the rings become thickened and lignified, the rings are not circular on their outer edges, but usually strongly angular, reflecting the position of the cell edges to the time when the rings became hardened. They are, however, displaced as the elements are stretched and new cell configurations are assumed by the remaining intact cells.

If trans-edge discontinuous openings are to be expected to form, they should form in the later matured portions of the primary xylem. This is usually the observed case, but there are a few exceptions. In *Angiopteris*, relatively late in the metaxylem one occasionally observes scalariformly bordered pits with their ends slightly crossing the cell edges. Similarly, in *Hibiscus*, lens-shaped pits in the elements of the late metaxylem protrude across cell edges.

Among the vascular plants, one finds various degrees of face conformance of openings in the secondary wall of tracheary elements. Where there is a transition from edge-continuous to edge-discontinuous openings, it often is a gradual one. Such transitions are illustrated by *Lycopodium*, *Angiopteris*, and *Hibiscus*. Hofmeister (1867) noted that elongated pits are usually just as wide as the cell faces.

It is suggested here that pitted elements with trans-edge alternate pitting represent modified reticulate elements in which the points of branching in the network have been shifted so that they fall along the cell edges and hence the openings fall on the faces. This interpretation is based on the transition of cell types found in the primary xylem of *Lycopodium* and in *Angiopteris*, and to a lesser extent on certain members of the Filicales where the elements are only in part trans-edge alternate. Saint-Pierre (1870) spoke of "vasseau rayés" and illustrated one as a helical element with some forks and a few anastomoses. He considered scalariform elements (scalariformly pitted elements) to be modifications of the "vasseau rayés" with superimposed regularity on its faces to become like a ladder. His statement is interpreted to mean essentially the same thing as is stated above, that is a shift in forks and anastomoses toward cell edges. However, this interpretation can only be applied to the trans-edge alternate scalariform elements, namely those of *Lycopodium*, the Marattiaceae, and to a slight extent the Filicales.

Elements with trans-edge opposite pitting are interpreted as representing elements with a basic framework in the form of a helix (simple or complex), or in the form of rings, or in the form of a reticulum in which the openings are elongate and cross cell edges. Opposite pits across cell edges would therefore have the same interrelationship as rowed pits within the faces. Such opposite pits, or in a broader sense rowed pits, are considered to have developed within the same primary pit area. Often the groups are outlined by the "bars" of Sanio as pointed out by Bailey (1919) who also regarded opposite pits as falling in the same primary pit area.

The term "pit area" when applied to tracheary elements, especially primary ones, must necessarily be used in a somewhat looser sense than when applied to thin-walled parenchyma cells. In the latter case they are well known structurally. In the former case they are poorly known, often defined only in terms of the "rims of Sanio" (*see* Bailey, 1919; Sifton, 1920). Esau (1953), who refers her information to Bailey by personal communication, states that pits may or may not be found over primary pit fields. When they are found over the fields, one or more pits may form over a single field. Similarly, pits may arise over primary wall parts that bear no primary pit fields. Esau (1953) states that "thus, there is no absolute interdependence between the position of the primary pit fields in the primary wall and the development of pits

in the secondary wall." The term " primary pit area " as used in the text above is used in a sense to denote an area over which the tracheary element has the potentiality of producing a pit as the result of differential secondary wall formation.

The term " sister pits " is introduced to apply to pits which may be referred to the same pit area. Here would not only be included the rowed pits, but also clustered pits as described by Bailey (1933) in *Cedrus*. The term " singleton " pits is similarly proposed to refer to pits where each one corresponds to an entire primary pit field.

A consideration of circular bordered pits and how they might have evolved seems apropos. In the genus *Lycopodium*, circular bordered pits are to be found in the early metaxylem and occasionally throughout the metaxylem to the exclusion of scalariformly bordered ones. The uniseriate trans-edge alternate arrangement of the pits, either circular or scalariform, and the transition of cell types from simple reticulate suggests only one possible interpretation, this being that the pits are all singleton pits and that in this genus the circular bordered pit is at the same level of phylogenetic specialization as is the elongate pit. In other words, the difference between the two kinds of pits is one of size only.

In the angiosperms, and certain fossil orders, it seems, as has been concluded on numerous occasions, that in most of the woody genera the circular pit has evolved as the result of a " breaking up " of elongate pits into a number of smaller ones. For a full account of the evidence see Frost (1931), Metcalfe & Chalk (1950). This interpretation seems at present too well documented to dispute.

That circular bordered pits are derived by the breaking up of scalariform pits has also been said of the Cordaitales (Bailey, 1925), a conclusion which seems justified as it is in the angiosperms. This conclusion has, however, been extrapolated to probable phylogenetic derivatives of the Cordaites, namely the Conifers, Taxads, *Ginkgo*, *Ephedra*, *Gnetum* and *Welwitschia*. In these extant plants, circular bordered pits appear in protoxylem elements between the kinds of thickenings which are more characteristic of protoxylem elements in general. In the transition of tracheary element types in the primary xylem of these plants, pits become more numerous, the openings in the secondary walls other than the circular bordered pits gradually fill in, in some cases both centripetally and tangentially, and eventually toward the end of the series the elements appear to have circular bordered pits in an otherwise continuous secondary wall. No scalariform or transitional or opposite pitting is to be found. Bailey (1925) interprets the circular bordered pits which occur here as having originated phylogenetically from scalariform pits by the familiar " breaking up " process, and, in the case of those occurring early in the series, as having worked back into the protoxylem and resulted in the elimination of typical scalariform and transitional pitting.

In *Botrychium* and *Helminthostachys* in the Ophioglossaceae one finds circular bordered pits appearing in the protoxylem elements. A transition of cell types follows in the later protoxylem and metaxylem culminating in, as in the gymnospermous plants mentioned above, a pitted element. Nowhere in the transition is there any suggestion of scalariform or transitional pitting. In *Ophioglossum*, however, in addition to the pits appearing in the protoxylem elements, one finds a succession of elements in the late protoxylem and metaxylem showing scalariform-reticulate and finally scalariformly pitted structure. There is no tendency for the scalariform pits to " break up " in the late metaxylem and form transitional or circular bordered pitting. In *Marattia*, one also finds a reticulate to scalariformly pitted transition, and in addition an occasional circular bordered pit in the reticulate elements. It is contended that in the Ophioglossaceae the circular bordered pit originated phylogenetically in the protoxylem or early metaxylem in ancestral forms in which there was in the later formed primary xylem a transition to scalariformly pitted element and that in *Botrychium* and *Helminthostachys* this transition was eliminated and replaced by a transition based on the elaboration of the pitted protoxylem elements.

In view of the existence side by side of these two types of transition in *Ophioglossum* and to some extent in *Marattia*, and the lack of evidence of pits "breaking up" in these genera, it seems justified to infer that the circular pits which appear in the early xylem elements of conifers, taxads, *Ginkgo*, *Ephedra*, *Gnetum*, *Welwitschia*, and also *Equisetum* (*see* Bierhorst, 1958) as well as the Ophioglossaceae evolved in the early xylem as circular bordered pits and not by way of scalariform bordered pits in the metaxylem.

Evidence for the existence of a structural framework in certain pitted elements upon which the pits are imposed is discussed above under the higher Filicales. A definite three-dimensional arrangement of pits in pitted elements where all faces are considered has long been recognized. Link (1839-43) recognized spiral structure and pit arrangement in a variety of types of tracheary elements. Similar recognitions were made by Hartig (1878), Luerssen (1881), Sanio (1863), Record (1925), and Alexandrov (1926). Ontogenetic transformation of a helical type tracheary element into a pitted type was suggested by Hartig (1878) and described in detail in terms of patterns of lignification by Alexandrov (1926) in *Ficus* and *Morus*. In the present paper a similar process is described for *Pteridium*.

Record (1925) states that alternate pits are arranged spirally while scalariform pits are in horizontal series. He interprets that opposite and scalariform pits are developed within an annular pattern. The transverse orientation is, however, no real criterion, since spiral thickenings may be essentially transversely oriented on a given face. Both Record (1925) and Jeffrey (1917) suggest a kind of merging of portions of spirals in the evolution of scalariformly pitted elements. Jeffrey (1917) suggests that from the spiral tracheid "by accentuation of the condition of approximation, fusion between bands results and we have as a consequence the presence of scalariform or reticulate tracheid". This interpretation can be accepted in part. It can possibly be accepted to a certain extent for application to the Marattiaceae, and Lycopodiaceae but to a much lesser extent for application to the Filicales and angiosperms. Jeffrey's interpretation can be applied without contradiction only in the case of scalariform elements which exhibit trans-edge alternate pitting. In the Filicales and angiosperms,[3] scalariformly pitted elements are mostly trans-edge opposite and where a basic helical pattern is discernible, it seems that the helical thickenings do not join directly between the elongate pits, but are united by extra secondary wall material. In other words, the helical thickenings are just as far apart where a pit is present as where one is absent in a given element.

Jeffrey's (1917) interpretation seems more applicable in the case of angiosperm reticulate elements than in the case of angiosperm scalariformly pitted elements. The transition of elements from helical to reticulate, which is mentioned by Weiss (1878) and Zimmermann (1930), along with the details of structure of certain types of reticulate elements indicates that many types of angiosperm reticulate elements may represent modified helical elements in which adjacent gyres are frequently joined as stated by Jeffrey. It follows that the trend to "approximation" and "fusion between bands" is expressed to a much greater extent in the intermediate members of the ontogenetic sequence (the reticulate members) than in the later members (the scalariformly pitted members) within some angiosperms and also possibly in some filicalean ferns. A high degree of reticulation ("approximation" and "fusion") probably does not occur even in the metaxylem of certain angiosperm families, e.g. Magnoliaceae and Commelinaceae. But again, this statement must be tested by future survey types of studies.

The observations and interpretations presented here emphasize the importance of restricting the concept of the primitiveness of "opposite pitting" over "alternate pitting" to those plant groups in which the conclusion is documented, namely the angiosperms. The same can be said of the primitiveness of scalariformly bordered pits over circular bordered

3. This generality may break down after this feature is looked for in more angiosperms.

pits. The interpretation that there is a phylogenetic trend from scalariform pitting to transitional pitting, to opposite pitting, and finally to alternate pitting (Bailey & Tupper, 1918; Brown, 1918; Frost, 1931) within the angiosperms is particularly well supported by the studies of Frost (1931). Following this interpretation, opposite pits must be regarded as sister pits, that is as having developed within the same pit area. This cannot be said of the apparently opposite pits which appear in the early metaxylem of *Pinus*. In many of the "lower vascular plants" circular bordered pits probably arose phylogenetically independently of scalariformly bordered pits, e.g. Ophioglossaceae, Equisetaceae, Conifers, Taxads, Ginkgoaceae, Gnetaceae, Ephedraceae, and Welwitschiaceae. Similarly, in several groups there is a range in pit size and shape from circular bordered to scalariformly bordered forcing one to infer that all pits in the range are at the same stage of phylogenetic specialization, e.g. *Lycopodium* and possibly *Psilotum*. The major difference between "alternate" and "opposite" pitting within the angiosperms is in the angle of the pit row with regard to the axis of the cell. (*see* Fig. 22 in Moseley, 1948, showing "alternate pitting" in *Casuarina*). Sifton (1920) concluded that in Cycads opposite and alternate pitting may be directly derived from scalariform pitting; this he based on orientation of the pit rows as compared to that of the scalariform pits. Bailey (1925) made a similar suggestion. The range in orientation of scalariform pits includes everything from transverse to vertical, often in the same plant. There is no evidence to indicate that phylogenetic changes in angle of orientation of scalariform pits or rows of shorter pits may not take place in both the direction of the horizontal as well as the vertical.

In certain fossil lycopods, vertical strands of cell wall material (the so-called "Williamson's striations"; *see* Duerden, 1933; Fry 1954; Barghorn & Scott, 1958) have been described as occurring between the larger transverse bars of wall material separating the scalariform openings. These strands have been variously interpreted. Two of the interpretations are: (1) that they represent secondary wall material (Duerden, 1933; Fry, 1954); and (2) that they represent primary wall material (Barghorn & Scott, 1958). For other views reviewed *see* Duerden (1933). The occurrence of minor vertical strands of cell wall material between major more or less transversely oriented strands of wall material is of widespread occurrence among vascular plants. In the Equisetaceae, they occur between annular thickenings (Bierhorst, 1958). Similarly, in the Ophioglossaceae, they occur between annular thickenings, but less regularly disposed and in fewer numbers than in *Equisetum*. Barghorn & Scott (1958) pointed out a condition similar to *Lepidodendron* and related forms in at least one extant angiosperm. There are instances in the Ophioglossaceae and Pinaceae where fine strands of wall material are inserted on a thin border of a bordered pit. The fine vertical thickenings of the Ophioglossaceae and Equisetaceae are, moreover, often of approximately the same dimensions as those in the fossil lycopods. Barghorn & Scott (1958) have insisted dogmatically that the Williamson's striations of fossil lycopods are a part of the primary wall. Their major reason for stating so is the apparent absence of lignin in the fine strands and the presence of the same in the major transverse thickenings which he has designated as secondary wall. It is quite clear, now, that a workable general concept of the primary as opposed to the secondary wall must in the interest of continuity be divorced from any consideration of lignification. Barghorn was apparently quite influenced by statements such as appear in Preston (1952) to the effect that the major chemical difference between the primary and the secondary wall is the presence in the latter and the absence in the former of lignin. Preston in all probability was referring to the primary wall as it was in the growing cell and not to the primary wall as it might be in older cells. Even the primary walls of protoxylem elements may after the period of elongation become quite lignified. Some readers may consider this statement contradicted by the generalization that the protoxylem elements lose

their living contents before elongation and therefore would not be expected to be able to synthesize more wall constituents. The generalization is, however, quite false. If it is at least partly true, it must be so of only early protoxylem elements and of only certain taxa. By a comparison of the Williamson's striations to similar structures in other vascular plants and by accepting the evidence of Fry (1954) from his electron microscope photographs that the strands are intimately connected in their submicroscopic framework to that of the major transverse bars, the interpretation that these are of secondary wall material comes quite naturally.

The dangers of relying on evidence from isolated sources such as single tissues or single organs to support phylogenetic conclusions are well known. These have been brought out in several publications by Bailey (e.g., 1953). Even so, it is always tempting to compare various plant groups with respect to isolated specific characteristics. If conclusions derived therefrom are to a certain extent in accordance with similar ones derived by using other very different kinds of evidence, then the probability of their correctness is greatly increased. With this in mind the following tentative conclusions have been reached. In terms of the structure of the primary tracheary elements:

(1) The living genera of Lycopods (*Lycopodium*, *Phylloglossum*, *Isoetes*, and *Selaginella*) are all phylogenetically relatively remote from each other. This conclusion has certainly been reached on numerous other occasions and is well supported by fossil record as well as comparative morphology.

(2) *Isoetes* is more like *Selaginella* than either one is like *Lycopodium*. This conclusion is based primarily on the presence in the first two genera of simple annular and simple helical elements as well as the reversed helical element, and conversely their absence in the last mentioned genus. This conclusion is in conformity with systems of classification in which the ligule is considered of prime importance.

(3) *Phylloglossum* and *Isoetes* are both specialized forms. This is certainly a generally accepted conclusion. Text descriptions will suffice as support.

(4) The two genera of the Psilotaceae (*Psilotum* and *Tmesipteris*) are quite closely related. Very few and relatively minor differences are to be found between the two genera in terms of their tracheary elements. Recent trends to erect two separate families (Pichi-Sermolli, 1959) seem quite unjustified.

(5) The Psilotaceae is remote from all other extant vascular plants. This is well supported by the peculiarities of their early annular and helical elements as well as the peculiar reticulate elements which appear later in ontogeny.

(6) The Equisetaceae is remote from all other extant vascular plants. See the descriptions of the tracheary elements in Bierhorst (1958).

(7) The three genera of the Ophioglossaceae (*Botrychium*, *Helminthostachys* and *Ophioglossum*) are closely related and form a uniform taxonomic group. This is based on the numerous characteristics of the protoxylem which they have in common.

(8) The three genera of the Marattiaceae studied form a uniform group; *Marattia* being more like *Danaea* than either of the two is like *Angiopteris*.

(9) The two genera of the Osmundaceae (*Osmunda* and *Todea*) are very close. The Osmundaceae in terms of its protoxylem is the most distinctive family among the leptosporangiate ferns.

(10) In terms of tracheary element structure, the Osmundaceae stands in a position intermediate between the higher leptosporangiate ferns and *Angiopteris* in the Marattiaceae.

(11) A fern with tracheary elements rather similar to those of *Angiopteris* may have given rise to the known Marattiales, the Ophioglossales and the Osmundaceae.

(12) If Cycads are genetically related to any of the living fern groups, their origin must be assumed from a level below the Ophioglossaceae and the Marattiaceae. There is no consideration here of whether or not the Cycads evolved from ferns by way of the Pteridosperms.

(13) Cycads show little or no relationship to *Ginkgo*, conifers, taxads or the "Gnetalean" genera.

(14) *Ephedra*, *Gnetum* and *Welwitschia* form a natural group, more closely inter-

related than any one of the three is related to any other known vascular plant.

(15) The taxads are relatively close to the conifers. The taxads and conifers are more closely related to each other than either one is related to any other group of known vascular plants.

(16) The group, *Ephedra, Gnetum, Welwitschia, Ginkgo,* taxads and conifers, is a natural taxonomic unit, and of monophyletic origin.

(17) Angiosperms probably did not arise from known Eusporangiate ferns.

(18) Angiosperms probably did not arise from conifers, taxads, *Ginkgo* or the Gnetales.

Summary

The early-formed tracheary elements of a variety of vascular plants have been described. The range in variation to be found among elements which have been categorically known as "annular", "helical", "reticulate", and "scalariform" is much more extensive than was formerly thought. Many of the specific variants are relatively specific for certain taxa. Several tentative phylogenetic speculations have been presented based on the occurrence of these variants. It has been found necessary to introduce a number of new terms because of new information and also because of ambiguities and variable usages in the previously published literature. A classification of tracheary elements has been formulated in which a minimum of new terms is utilized. The concept of the primary cell wall in terms of stretchability is strongly supported. The flowering plants were barely considered in this study; however, the study strongly indicates that critical survey type studies of the primary xylem elements within the angiosperms should prove extremely rewarding and valuable.

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THE MORPHOLOGY AND EMBRYOLOGY OF *PINUS ROXBURGHII* SAR. WITH A COMPARISON WITH *PINUS WALLICHIANA* JACK.

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Five species of *Pinus* namely, *P. roxburghii*, *P. gerardiana*, *P. wallichiana*, *P. insularis* and *P. merkusii* grow in India. Of these *P. roxburghii* is the most commonly cultivated. The timber is used for various purposes like 'deal' boxes and cheap furniture. Systematic tapping of the resin is done in east and west Almora, Nainital (Uttar Pradesh) and in certain places in the Panjab. The distillation of oleoresin yields about 20 per cent oil of turpentine and 80 per cent colophony or rosin. The grade and quality of rosin determines its use. The best grades are used for varnishes and to a small extent in medicine as a stimulant, stomachic and remedy for abscesses (Chopra *et al.*, 1957). Considerable quantities of rosin are employed in paper sizing and soap manufacture. The poorer grades which are darker in colour are employed in the manufacture of linoleum. A part of it is also distilled to yield rosin spirit and rosin oil (Howes, 1949).

The tree is distributed in the outer ranges and principal valleys of the Himalayas from 1,500 feet to 7,000 feet (Figs. 1, 2). It occurs in the lower ranges of the western as well as the eastern Himalayas extending to Bhutan and Sikkim and forming pure forests at places. At higher and lower altitudes it usually forms mixed forests with different plant communities.

Previous Work

The literature on *Pinus* has already been reviewed by Konar & Ramchandani (1958). Lyons (1956) studied seed production in *P. resinosa* and Takao (1959) has made a cytochemical study on the proteid vacuoles in the egg of *P. thunbergii*.

FIG. 1 — Map of Indian continent showing the distribution of different *Pinus* species.

Material and Methods

Some embedded material of *P. roxburghii* collected from Agra and Simla was very kindly passed on to me by Professor P. Maheshwari. More than a hundred and fifty collections were made personally from trees growing near the Vidhan Sabha in Vijay Chowk, New Delhi.[1] The procedure for fixation and microtomy was the same as described for *P. wallichiana* (*see* Konar & Ramchandani, 1958).

1. Thanks are due to Dr G. S. Randhawa, Deputy Director of Horticulture, North Division, C.P.W.D., New Delhi, for allowing me to make necessary collections from the gardens under his control.

Morphology

There are two types of branches — the branches of unlimited growth or long shoots and the branches of limited growth or dwarf shoots (Fig. 3). In the seedling stage the long shoot bears a whorl of 8-14 cotyledonary leaves. These are 2-6 cm long, acicular, obscurely triquetrous and pale green with sheathing leaf bases. Abscission occurs where the leaf departs from the stem and the persistent base is easily recognized. Next come the so-called juvenile leaves. When the plants are about one and a half to two years old, dwarf shoots appear in the axils of juvenile leaves but are hardly more than a milli-

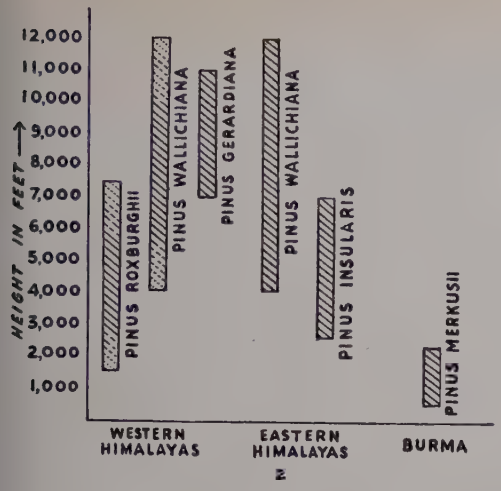


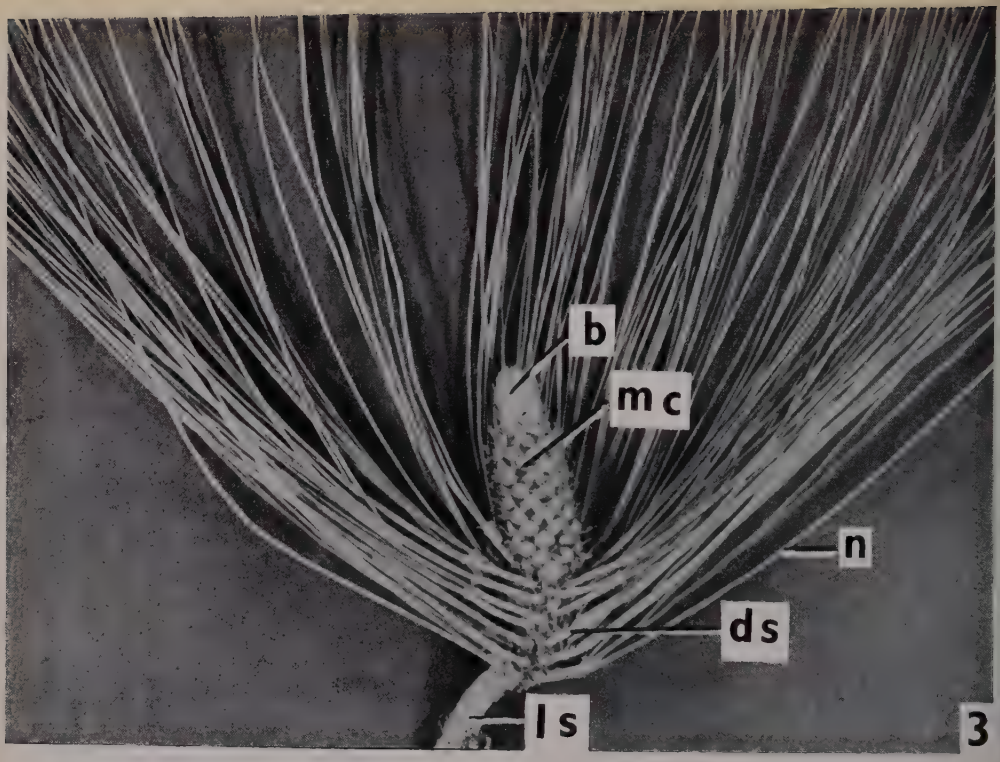
FIG. 2 — Altitudinal distribution of *Pinus* species in the western and eastern Himalayas and Burma. Density of line indicates relative frequency.

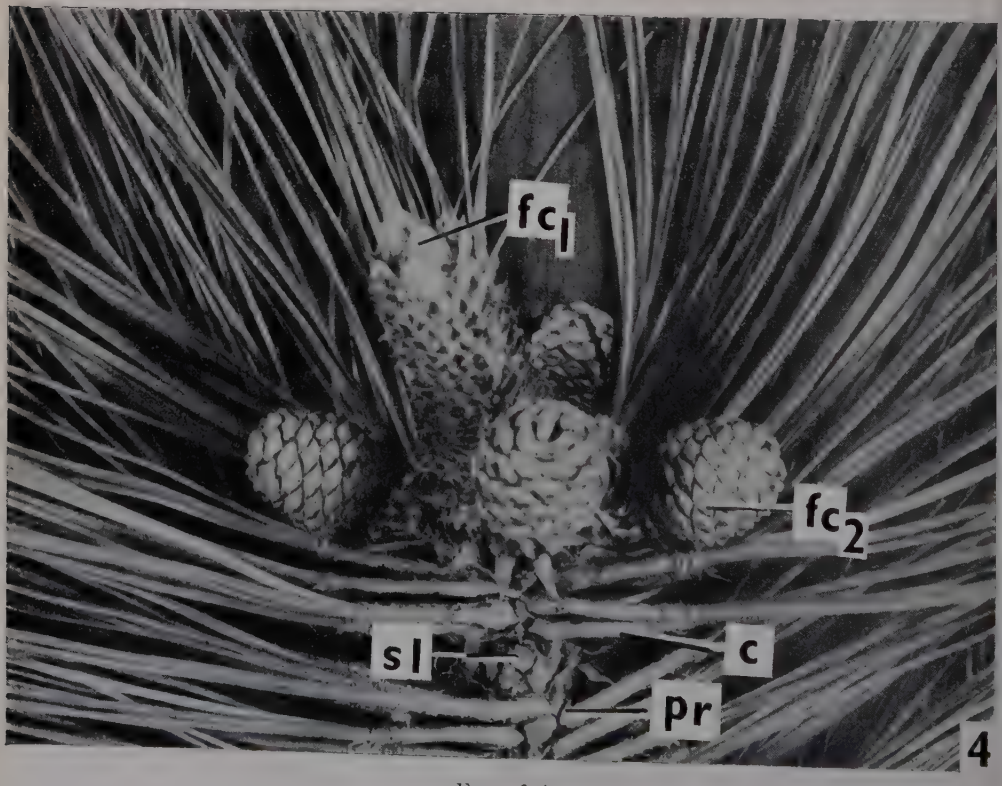
meter in length. In a mature plant the dwarf shoots arise in the axils of scale leaves. Each dwarf shoot bears the usual prophylls and 8-10 spirally arranged, persistent cataphylls (*see* also Konar & Ramchandani, 1958). They are initially green in colour but later turn brown. The dwarf shoots bear three (Figs. 3, 4) needle-like leaves which are 12-20 cm long and triangular in cross section. The dwarf shoots are initiated in March-April but unfold in the following April soon after the pollen is shed. The needles attain their maximum length by the beginning of September. With further growth the basal part of the plant sheds its leaves and is covered by rough bark.

The male cones, 120-140 in a cluster, are initiated in September (Delhi) and are arranged spirally (Fig. 3). Each male cone arises in the axil of a scale leaf which falls off when the cone is mature (Fig. 5). The bracts persist since they are held between the tightly packed cones. Several bracts cover a male cone when young. Each cone bears 100-136 microsporophylls which are spirally arranged. The tips of the microsporophyll bend upwards and become scaly. Two microsporangia are borne abaxially. At maturity they show a prominent line of dehiscence which is two cells wide and runs all along the long axis of the microsporangium. The first shower of pollen takes place about the second week of March and continues for about fifteen days. A male cone with mature pollen is about 1 cm long but just prior to shedding the central axis elongates considerably, specially at the base, and reaches a length of 3-4 cm.

The female cones are restricted to the upper branches of the tree and are pale green at the time of emerging (Fig. 4). The tip of the stem continues to grow and regains its apical position. Generally one or two female cones are borne on a shoot but occasionally as many as four may develop (Fig. 4).

Towards the beginning of March, the female cones emerge from the enclosing scale leaves (Figs. 17, 18). Prior to pollination the bract scale is larger than the ovuliferous scale and they arise more or less at right angles to the cone axis (Figs. 17, 18), but the ovuliferous scale soon outgrows the bract. After pollination the female cone slowly turns brown. Due to rapid growth and swelling of the ovuliferous scale in the subapical region, the cone becomes closed. At the region of swelling, the upper and lower epidermis develop hairs which become interlocked with similar ones belonging to the scales immediately above and below. There is further secretion of resin which soon dries up and contributes to an effective closure of the cone. This prevents the drying up of the ovules. The cones remain in this condition till the beginning of the second year (Fig. 4). Later, when they restart their activity, the green colour is regained. The cones now increase in size until fertilization, finally turning brown once more when the embryo has been formed. In the mature cone the bract scale is seen as a small membranous structure at the base of the ovuliferous scale. The outer surface of the cone shows the rhomboidal ends of the ovuliferous scales each with a small raised point known as the umbo. Soon after pollination the ovuliferous scales harden still further due to the thickening of the cell walls. Plenty of resin oozes out from the edges of the ovuliferous scales and can be seen in the form of large shining drops.





FIGS. 3-4.

Life History

MICROSPORANGIUM — Towards the beginning of September (Delhi) a mass of hypodermal archesporial cells becomes differentiated which can be recognized by their larger size and more conspicuous nuclei. These cells divide to give rise to a large number of cells (Fig. 6). The primary wall layer which is cut off at the periphery of this tissue (Fig. 7) divides anticlinally and periclinally to give rise to three or four layers of cells. By further divisions the archesporial cells form the sporogenous tissue. During December and January (the coldest months at Delhi) activity is reduced to a minimum.

Further development of the microsporangium is similar to that of *P. wallichiana* (*see* Konar & Ramchandani, 1958). Although all the sporogenous cells are potentially capable of giving rise to microspores, several of them degenerate and are absorbed by the developing microspores. Towards the beginning of February the cells enter meiosis (Figs. 8, 9) and finally give rise to microspore tetrads (Fig. 10).

The uninucleate pollen grain is the first cell of the male gametophyte (Fig. 11). There is the usual development of the wings or sacci (Figs. 11-14) as in *P. wallichiana* (Konar & Ramchandani, 1958). The pollen is shed at the four-celled stage. A mature grain shows the usual cappa, cappula and tenuitas as described for *P. wallichiana* (Konar & Ramchandani, 1958).

MEGASPORANGIUM — Towards the beginning of February, the female cone consists of a broad axis with slight elevations. These represent the initiation of the bract scales. By the middle of February a slight hump of tissue appears above each bract scale (Fig. 20) and grows rapidly to give rise to the ovuliferous scale. By the third week of February a pair of ovules makes its appearance on it (Figs. 21, 22).

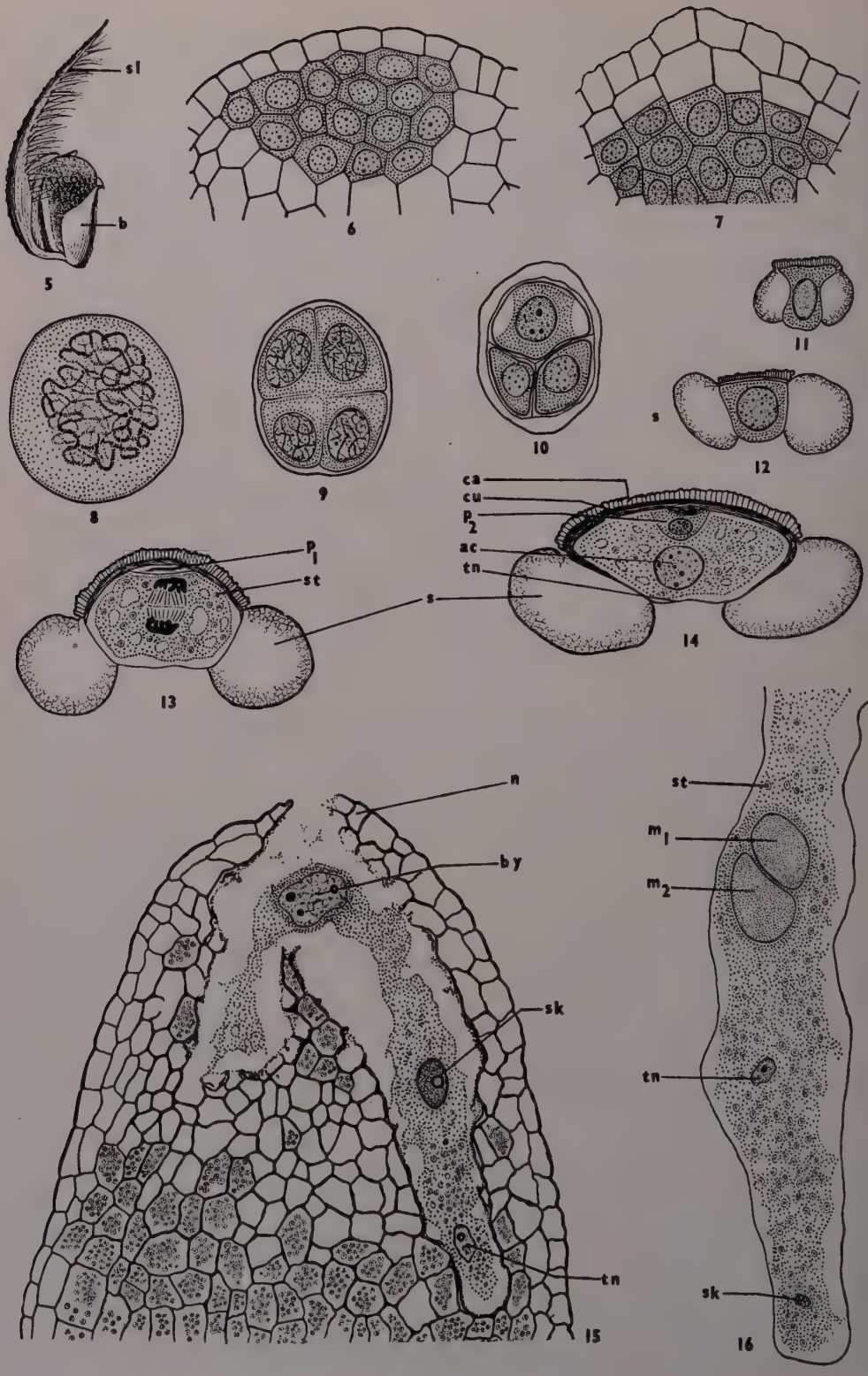
The ovule is unitegmic and crassinucellate (Fig. 22). The nucellus is free from the integument except at the chalazal end (Fig. 22). The integument continues into a tube, well beyond the level of the nucellus. The micropylar canal is fairly broad and its edges extend into two long arms. Initially they are curved in but at the time of pollination they are flayed out. The nucellus is broader at the micropylar than at the chalazal end.

A hypodermal archesporial cell differentiates by the third week of February. It soon divides periclinally into a primary parietal cell and the megaspore mother cell (Fig. 23). Occasionally more than one archesporial cell may be formed. The primary parietal cell undergoes many divisions so that the mother cell or cells are pushed deep into the nucellus. The megaspore mother cell undergoes the usual reduction divisions to form a linear tetrad (Figs. 24, 25). The three upper megaspores of the tetrad degenerate and only the lowest functions. The formation of tetrads takes place during the middle of March.

Meanwhile the cones have been pollinated, the pollen landing in a slight depression at the tip of the nucellus. Towards the middle of March, 3-5 layers of cells with dense cytoplasm and prominent nuclei become differentiated around the megaspore mother cell. They form the spongy tissue. In those ovules in which the megaspore mother cell or the megaspore fails to function, the cells of the surrounding tissue swell and grow in,

←

FIGS. 3-4 — (*b*, bud; *c*, cataphyll; *ds*, dwarf shoot with prophylls and cataphylls; fc_1, first year female cone enclosed within scale leaves; fc_2, second year female cone; *ls*, long shoot; *mc*, male cone; *n*, needle; *pr*, prophyll; *sl*, scale leaf). Fig. 3. A long shoot bearing clusters of male cones, unopened dwarf shoots and terminal bud. × 0·25. Fig. 4. A long shoot bearing shoot of current year and female cones of first and second year (the first year cones are still within the covering scales). × Natural size.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FIGS. 5-16.

giving the false appearance of the presence of a developing gametophyte. Finally, however, they degenerate.

POLLINATION — At the time of pollination the two long arms of the integument are curved out. The pollination drop is secreted at night; this catches and draws in the wind borne pollen (*see* also Doyle & O'Leary, 1935; McWilliam, 1958). Soon after pollination the micropylar canal is closed due to division and enlargement of the cells in the subapical region. The closed aperture has a slit-like form. The pollen tube is given out from the tenuitas and enters the nucellus. The tube nucleus migrates into the pollen tube while the antheridial cell remains in the pollen grain.

FEMALE GAMETOPHYTE — The ovule as well as the pollen tube inside the nucellus resume growth only in February next. The central cavity of the female gametophyte is greatly enlarged and is lined by a large number of free nuclei. The spongy tissue can be clearly seen to start with, but as the archegonia are initiated it is gradually absorbed.

As the number of nuclei in the female gametophyte increases (Fig. 26) the megaspore membrane thickens and develops a striated exine and a smooth intine (Fig. 26). Wall formation is centripetal and ensues when nearly two thousand and five hundred nuclei have been formed.

ARCHEGONIUM — The archegonial initials, generally 2-4, arise from the superficial cells at the micropylar end of the gametophyte. Later development is similar to that noted in *P. wallichiana* (Konar & Ramchandani, 1958). With the development of the archegonium there is a growth of the gametophytic tissue surrounding the neck cells so that the neck becomes lodged in a cavity (Figs. 27-31).

At the time of fertilization (end of April or beginning of May) the archegonium shows four neck cells arranged in one tier (Figs. 29, 30), a degenerated ventral canal cell and an egg with a large central nucleus and numerous proteid granules (Fig. 31). The fibrils around the egg nucleus disappear which now becomes surrounded by dense cytoplasm.

RENEWED ACTIVITY OF THE MALE GAMETOPHYTE IN THE SECOND YEAR — The resting pollen tube renewes its activity in the nucellus towards the end of March. The apical end of the nucellus consists of cutinized cells; those just below are richly cytoplasmic and divide repeatedly. As these cells divide and grow, the nucellus becomes cone-like. In the pollen grain the antheridial cell divides to form the stalk and body cells. The cytoplasm of the stalk cell is vacuolated while that of the body cell becomes dense (Fig. 15). The stalk and the body cells migrate into the pollen tube. The body cell divides to give rise to two male nuclei enveloped in a common mass of cytoplasm. Due to unequal growth, one of the male nuclei becomes larger in size than the other (Fig. 16).

FERTILIZATION — A few days before fertilization the pollen tube grows very rapidly and reaches the neck of the

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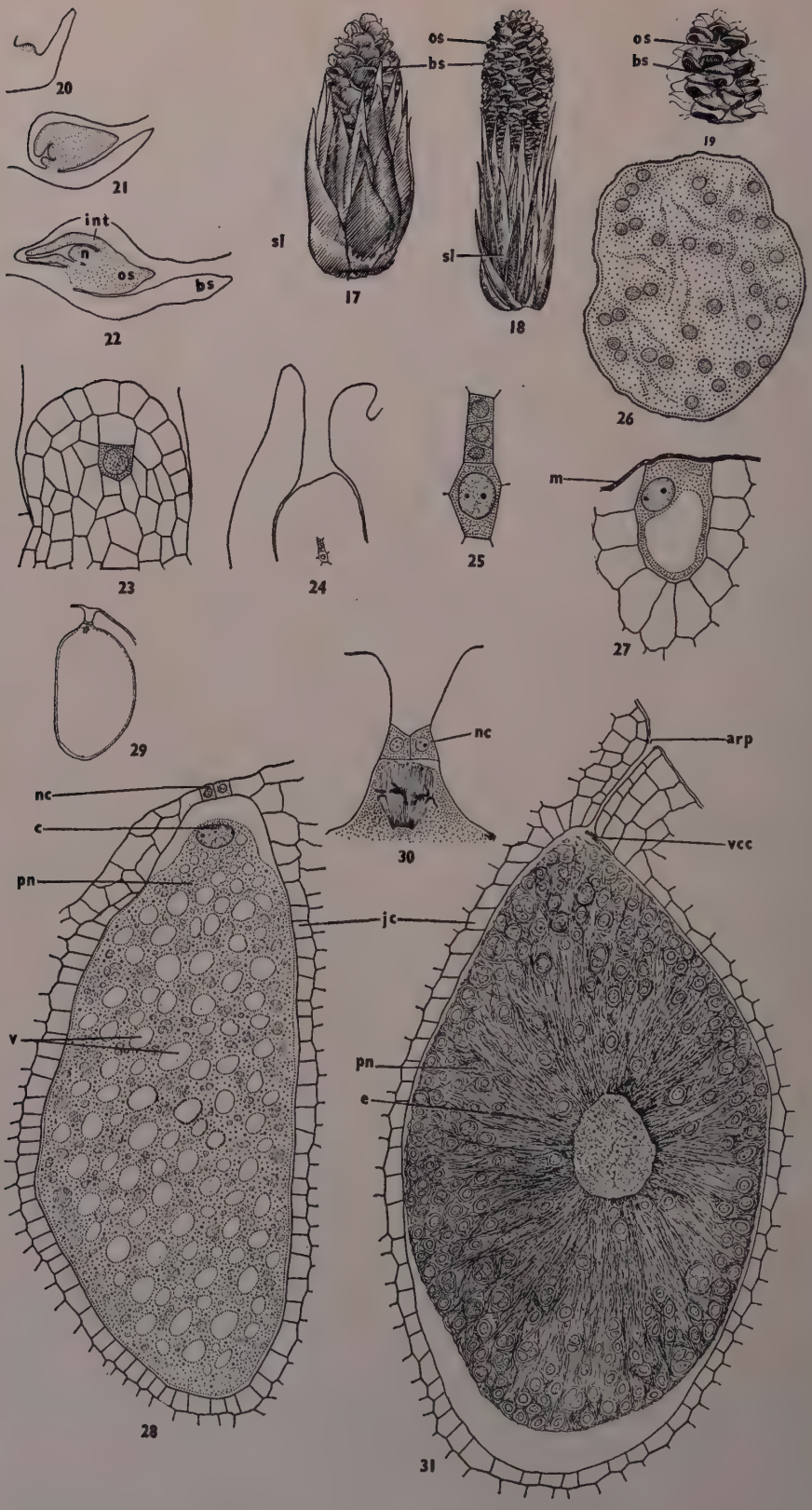
FIGS. 5-16 — (*ac*, antheridial cell; *b*, bract; *by*, body cell; *ca*, cappa; *cu*, cappula; m_1, first male cell; m_2, second male cell; *n*, nucellus; p_1, first prothallial cell; p_2, second prothallial cell; *s*, saccus; *sl*, scale leaf; *sk*, stalk cell; *st*, starch grain; *tn*, tube nucleus). Fig. 5. A male cone borne in the axil of a scale leaf and partially covered by bracts (March 3, 1957). × 5. Fig. 6. A part of l.s. microsporangium showing a mass of hypodermal archesporial cells (Sept. 5, 1956). × 430. Fig. 7. Slightly advanced stage, primary wall layers and sporogenous cells have been formed (Oct. 1, 1956). × 430. Figs. 8-10. Stages in Meiosis (Feb. 10, 1957). × 640. Fig. 11. Young microspore (Feb. 18, 1957). × 640. Figs. 12-14. Stages in the development of the microspore (Feb. 25, 1956). × 640. Fig. 15. Pollen tube within a nucellus. The stalk cell has detached itself from the body cell and is migrating ahead (Apr. 28, 1956). × 180. Fig. 16. A part of the pollen tube showing two unequal male nuclei with a common cytoplasm, the tube nucleus and the stalk cell (May 5, 1956). × 180.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archegonium. Fertilization is effected in the same manner as described for *P. wallichiana* (Konar & Ramchandani, 1958).

EMBRYOGENY — The development is similar to that in *P. wallichiana* but no rosette embryos are formed in *P. roxburghii*.

The embryonal cells undergo very rapid divisions to give rise to a mass of small cells forming a cylindrical structure. The cells of the proximal end row divide predominantly in the transverse plane while those at the distal or terminal end undergo anticlinal, periclinal and oblique divisions. Such cells of the proximal region which do not contribute to the formation of the root cap and root initials are added on to the secondary suspensors.

The epicotyl-root axis shows two distinct zones as mentioned by Spurr (1949). The first is the covering tissue of the root cap consisting of obliquely arranged cells. The oblique arrangement gradually diminishes towards the central region where the cells are vertically arranged and are said to form the column of the root cap. Here the divisions are mainly in the transverse plane.

The root region is followed by the hypocotyl-shoot axis showing a well-marked pith. Surrounding this are 2-3 layers of elongated cells which constitute the procambium. The outer limit of the procambium can be approximated with the development of the secretory cells referred to by Spurr (1949). Gradually there is a differentiation of the cortex, cotyledons and the shoot apex. The cotyledons are traversed by the procambium and a mesophyll. The mature embryo has a distinct epicotyl-root axis and a hypocotyl-shoot axis bearing several cotyledons. Generally one embryo matures but sometimes even two may reach maturity.

Initially the integument comprises 3-5 layers (Fig. 32) but with the growth of the ovule it becomes several layered (Fig. 33). Finally it is differentiated into the usual outer fleshy, middle stony and inner fleshy layers (Fig. 34) as described for *P. wallichiana* (Konar & Ramchandani, 1958).

GERMINATION OF SEED — The seed germinates in 20-25 days after sowing. Germination can be hastened by using acid soaked saw dust (Konar, 1958). The hypocotyl becomes arched so as to carry the cotyledons and the seed coat above it. The cotyledons continue to absorb food from the seed until the latter has been exhausted after which the seed coat drops off. The epicotyl, deep within the whorl of cotyledons, gives rise to the stem and leaves. The cotyledons persist for a long time dropping off only after the juvenile leaves and long shoot have grown considerably.

COMPARISON WITH *P. wallichiana* — The following table gives a comparison of the existing data on the distribution, general morphology and life history of the two principal Indian species, *P. roxburghii* and *P. wallichiana*, investigated in this laboratory:

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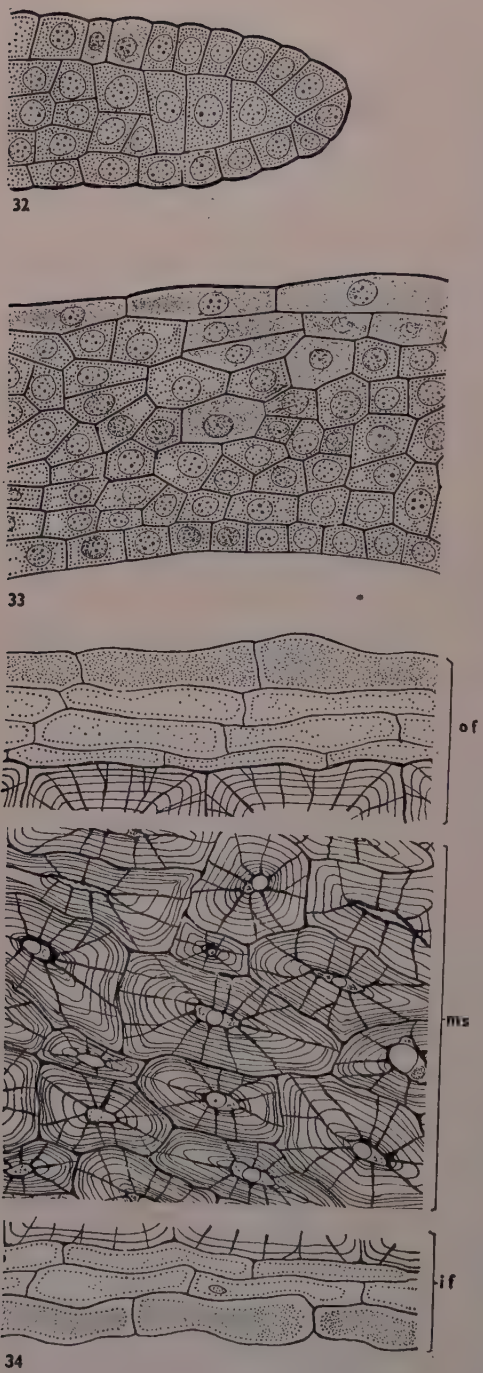
FIGS. 17-31 — (*arp*, passage of the archegonial neck; *bs*, bract scale; *c*, central cell; *e*, egg; *int*, integument; *jc*, jacket cell; *m*, megaspore membrane; *n*, nucellus; *nc*, neck cell; *os*, ovuliferous scale; *pn*, paranucleus; *sl*, scale leaf; *v*, vacuoles; *vcc*, ventral canal cell). Fig. 17. A young first year cone pushing out of its covering scales. × 1·5. Fig. 18. An open stage of a first year female cone (Feb. 15, 1956). × 1·5. Fig. 19. An enlarged view of the ovuliferous and the bract scales (Feb. 6, 1956). × 1·5. Figs. 20-22. Stages in the initiation and development of the ovule (Feb. 12, 1957). × 40. Fig. 23. Nucellus with primary parietal cell and the primary sporogenous cell (Feb. 20, 1956). × 260. Figs. 24-25. Formation of a linear tetrad. Figure 25 is a portion enlarged from Fig. 24. × 20; × 115. Fig. 26. Whole mount of a free nuclear gametophyte (Feb. 20, 1956). × 115. Fig. 27. An archegonial initial (Mar. 11, 1956). × 115. Fig. 28. A young vacuolated archegonium (Apr. 4, 1956). × 115. Figs. 29-30. Division of the central cell (Apr. 22, 1956). × 115. Fig. 31. A mature archegonium with degenerating ventral canal cell and a large egg (Apr. 28, 1956). × 115.

TABLE 1

	PINUS ROXBURGHII	*PINUS WALLICHIANA*
Distribution and General Morphology		
1. Distribution	Western Himalayas, Nepal, Bhutan and Sikkim, at 1500-7000 ft.	Western Himalayas, Nepal, Bhutan, Sikkim and extend to North East Frontier Agency, at 5000-11000 ft.
2. Bark	In young trees — dark grey, fissured deeply, non-resinous In older trees — thick and dark reddish-brown in colour, deeply fissured	In young trees — greenish white, thin, smooth and resinous In older trees — thick, greyish-brown, shallowly fissured
3. Winter buds	Ovoid, small, not resinous. Protected by closely pressed brown scales with fibrillar margin	Cylindroconic, small, matted with resin, scale leaves with fibrillar margin
4. Young shoots of unlimited growth	Grey or pale brown, covered with scale leaves which persist for several years	Light brown, deciduous scale leaves
5. Dwarf shoot	Persistent	Persistent
6. Prophylls & cataphylls	Persistent and with fibrillar margins. Forming a covering all around the dwarf shoot enclosing the basal part of the needles	Deciduous and with minutely fibrillar margins. Initially form a loose whorl around the base of the needles
7. Needles (Leaves)	Persistent, lasting for 1-3 years, tough, deep green, 23-35 cm long, margins minutely toothed, apex narrowing into a fine point, 3 needles per cluster	Persistent, lasting for 3-4 years, thin and delicate, greyish-green, 12-20 cm long, margin minutely toothed, apex sharply pointed, 5 needles per cluster
8. Male cones	Cluster of 120-140 male cones arranged spirally. Each cone situated in the axil of a prominent brown scale leaf and covered over by four prominent brown covering scales and several smaller scales. Cone globular when young but becoming elongated at maturity. Number of microsporophylls 90-130	Cluster of 30-35 cones arranged spirally. Each arises in the axil of a light green scale leaf and covered over by 10-12 equally prominent greenish-white scales. Cone conical when young but elongated at maturity. Number of microsporophylls 85-115
9. Female cone	Young female cone prior to pollination is an ovoid structure covered by involucral bracts which persist for a year	Young female cone prior to pollination is an elongated structure covered by numerous involucral bracts which fall off soon after pollination
	At time of pollination the emergent cones are pale green turning light brown soon after. With renewed growth they again turn green finally turning brown once more	At time of pollination the emergent cones are deep pink turning greenish-brown soon after. Become green once again in following year and finally turn brown at maturity
	Stalk of the cone does not elongate after pollination	Stalk of cone elongates considerably after pollination
	Mature cone conical, 11-21 cm long and 6-10 cm broad at base; scales hard and woody; and the exposed part (umbo) elongated, thickened and reflexed; 95-115 spirally arranged pairs of bract and ovuliferous scales	Mature cone greatly elongated, cylindrical, 15-30 cm long and 3-5 cm in diameter; umbo rudimentary; scales not as hard as in *P. roxburghii*; 80-90 spirally arranged pairs of bract and ovuliferous scales
	1·0-1·3 cm long with a wing 2·5-3·0 cm long	0·5-0·9 cm long with a wing 2·0-2·5 cm long

TABLE 1 — *contd.*

	PINUS ROXBURGHII	*PINUS WALLICHIANA*
Microsporogenesis and Male Gametophyte		
10. Initiation of male cone	Early September	Middle of October to the beginning of November
11. Formation of wall layers and divisions in sporogenous cells	October	Beginning of April
12. Differentiation of tapetum	Middle of November	Beginning of April
13. Division in microspore mother cells	Early February	Early April
14. Formation of tetrads	Early February	Early May
15. Development of endothecium and degeneration of other wall layers	Middle to end of February	Middle to third week of May
16. Uninucleate pollen grain	End of February	Middle to third week of May
17. Maturation and shedding of pollen	Middle to end of March	End of May to beginning of June
18. Germination of pollen on the nucellus	Soon after shedding	Soon after shedding
19. Period of rest	Approximately 10 months (May to February next)	Approximately 10 months (June to March next)
20. Division of generative cell to form the stalk and body cells	Beginning of March II	Not investigated
21. Migration of the stalk and the body cells into the pollen tube	Middle of March II	Third week of May II
22. Division of the body cell into two male nuclei	Middle of March II	End of May II
23. Fertilization	April II	End of May II to beginning of June II
Megasporogenesis and Female Gametophyte		
24. Initiation of female cone	Early February	Not investigated
25. Differentiation of hypodermal archesporial cell	Early February	Not investigated
26. Reduction divisions	Middle of February	Third week of April
27. Emergence of female cone	End of February to beginning of March	Beginning of May
28. Pollination	Middle to end of March	Middle of May to beginning of June
29. Closure of micropyle and female cone	End of March	Beginning of June
30. Free nuclear divisions in the functional megaspore to produce 16-32 nuclei	End of March to beginning of April	June
31. Period of rest	9 months	8 months
32. Renewed activity	Beginning of February II	Beginning of February II
33. Growth of gametophyte	Till the middle of March II	Till the third week of April II
34. Initiation and enlargement of archegonial cells	End of March II	Beginning of May II
35. Maturation of archegonia	Middle to 3rd week of April II	Middle of May II
36. Fertilization	Fourth week of April II	End of May II to beginning of June II
37. Mature proembryo	Early May II	Early June II
38. Period of embryonal competition	Four weeks	Seven weeks
39. Development of embryo	Till December II	Till December II
40. Opening of cone and shedding of seeds	April III to May III	December II



FIGS. 32-34—(*if*, inner fleshy layer; *ms*, middle stony layer; *of*, outer fleshy layer). Progressive stages of development of the seed coat. × 430.

Discussion and Summary

Of all the genera of the Pinaccae[2] the genus *Pinus* is the most well represented in India. *Pinus roxburghii* is one of the low altitude pines ranging in distribution from 1500 to 7000 feet.

The plant bears the usual long and dwarf shoots, and the prophylls, cataphylls and needles.

The male cones are borne in clusters of 120-140 members. There are about 135 microsporophylls per male cone. The female cone consists of spirally arranged bract and ovuliferous scales. The stalk of the female cone does not elongate after pollination as seen in *P. wallichiana*.

The development of the wall layers and sporogenous tissue is similar to those in *P. wallichiana*. Ferguson (1904) was of the opinion that the tapetum appeared to originate from the outermost wall layer and Sethi (1929) failed to make any specific mention to this point. The present investigation clearly demonstrates the origin of the tapetum from the innermost of the wall layers.

Wall formation in the tetrads is simultaneous as observed by Ferguson (1904) and Chamberlain (1935) in the species studied by them. This does not support the observations of Sethi (1929) who described an ephemeral cell wall after the first meiotic division.

The pollen is shed at the four-celled stage as noted by Ferguson (1904) and Johri (1935) and not at the three-celled stage as claimed by Sethi (1929).

The female cones start emerging from the scale leaves towards the beginning of March. Pollination takes place in the middle of March. My observations conform with those of Doyle & O'Leary (1935) who have described the mechanism of pollination in detail.

The pollen grains germinate on the nucellus. Immediately after the formation of the pollen tube, the tube nucleus migrates into it.

The female cone closes soon after pollination. The closure of the female

2. Hitherto the family comprised 9 genera. A recent addition is *Cathaya*, described from China (Chun & Kuang, 1958).

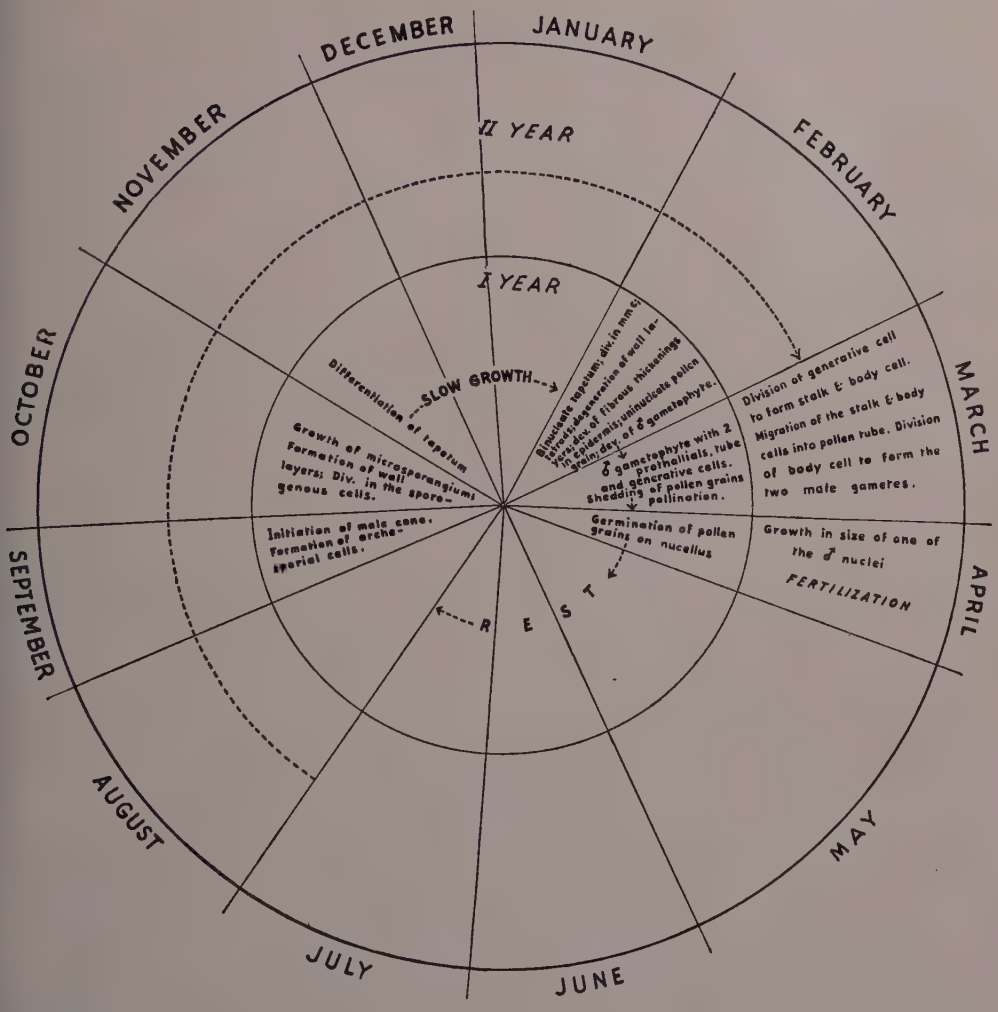


FIG. 35 — Life cycle chart to show microsporogenesis and male gametophyte development.

cone is due to a swelling of the ovuliferous scale on the dorsal as well as the ventral side and the development of the multicellular hairs on either side. The cone is further sealed due to secretion of resin.

A hypodermal archesporial cell differentiates in the nucellus and cuts off the primary parietal cell and the primary sporogenous cell. The megaspore mother cell becomes deep-seated due to the formation of parietal tissue. A linear tetrad of megaspore is formed of which the upper three degenerate and the lowest functions. Earlier workers like Ferguson (1904) and Sethi (1929) failed to trace the hypodermal origin of the archesporium, perhaps due to lack of sufficiently young stages. At the time of emergence of the female cone out of the covering scales the ovules already show a deep-seated megaspore.

Surrounding the megaspore tetrad or functional megaspore 2-3 layers of prominent cells differentiate into a spongy tissue. The usual free nuclear divisions occur followed by wall formation. The

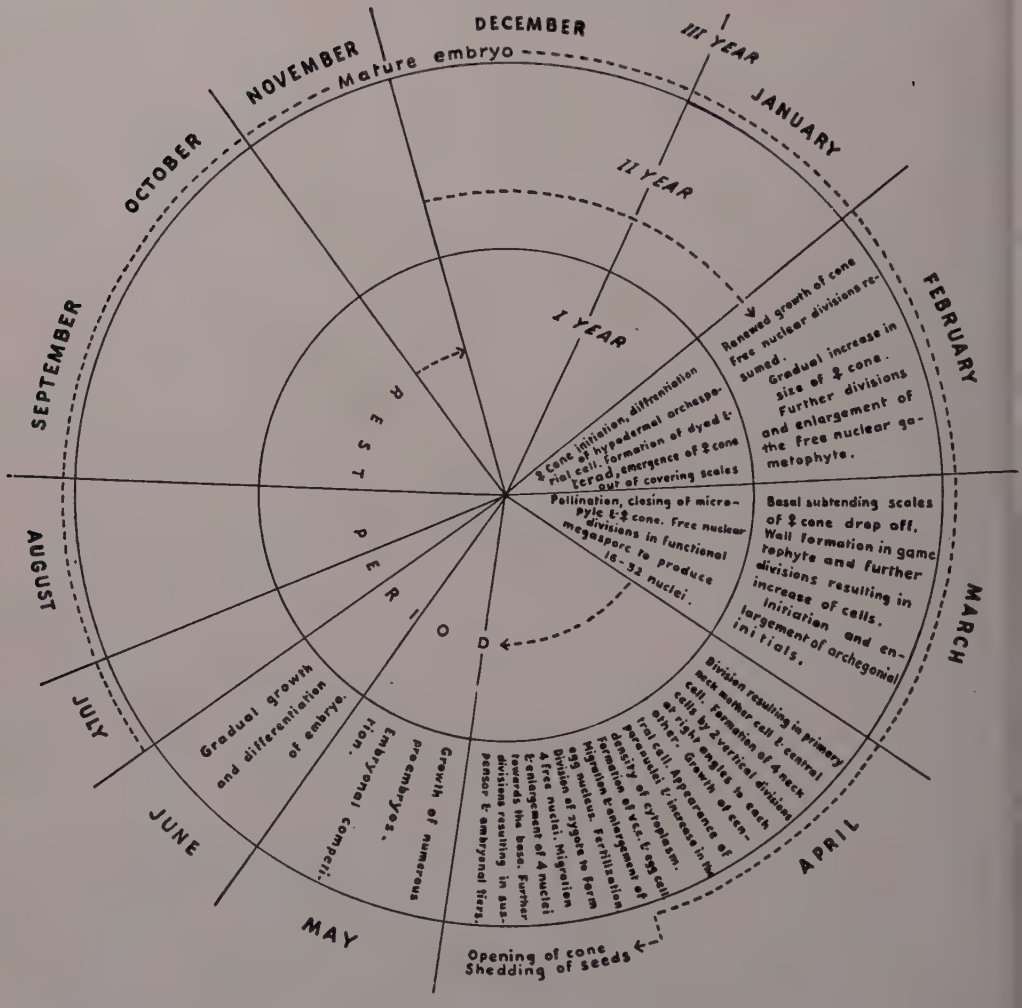


FIG. 36 — Life cycle chart to show megasporogenesis, female gametophyte and embryo development.

archegonial initials develop into mature archegonia similar to those of other pines.

The antheridial cell divides to form the stalk and the body cells. The latter divides to form the two male nuclei enveloped in a common mass of cytoplasm. A pollen tube just prior to fertilization shows the tube nucleus, the stalk cell and the two unequal male nuclei enveloped in a common mass of cytoplasm.

Fertilization and development of the embryo resemble other pines. The seed coat develops in the same way as in *P. wallichiana*. The seed germinates within 20-25 days of sowing.

Figures 35 and 36 show the time schedule in the life history.

I take this opportunity to express my deep sense of gratitude to Professor P. Maheshwari under whose guidance and encouragement this work was carried out. To Mr D. M. Sonak I am grateful for sketching a few morphological figures.

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REVIEWS

ESAU, K. 1960. "Anatomy of Seed Plants." Pp. 376. John Wiley and Sons, Inc., New York. $ 6.95.

THE appearance in 1953 of Esau's *Plant Anatomy*, the outstanding book in its field, seemed to preclude the publication of another English treatise on this subject for a number of years. However, Professor Esau has been prevailed upon — above and beyond the call of duty — to write a condensed version intended specifically as a text for standard courses in plant anatomy. The result, *Anatomy of Seed Plants*, is a handy book about half the size of its predecessor, yet it covers the same topics. It is not an abridged edition of the more comprehensive work but is reorganized and rewritten in a more concise style omitting some details, particularly historical background and derivation of terms. Much reduction was accomplished through the logical expedient of incorporating the cytology into the appropriate chapters dealing with the various cell and tissue types, thus avoiding much repetition. Likewise, apical meristems are treated, not as a separate topic, but as an integral part of the ontogeny of root and stem. On the other hand, the subject of embryos has been expanded into a full chapter which appears, and rightly so, as the first topic in the book rather than being placed at the end in the discussion of the seed. This is followed by a chapter entitled "From the Embryo to the Adult Plant". These two chapters serve as an introduction to the concepts of growth, differentiation and organization. The topics root and stem have each been split into two chapters, one dealing with the primary body and the other secondary structure. The leaf also appears in two parts, the survey of variation in form following the chapter on basic considerations. Actually there are two more chapters in this book than in the larger treatise, making it more suitable as a text by allowing more flexibility in choice of sequence of presentation, although the one given is very commendable. In this regard, it was a fortunate decision to introduce the root before the stem and leaf, because, as the author points out, the relative simplicity of root structure makes it easier to comprehend histological organization. Furthermore, an acquaintance with the concepts pericycle and endodermis as seen in roots is prerequisite to a proper introduction to the stelar theory.

Undoubtedly, the feature of this book that will be most appreciated is a much needed glossary defining 691 terms. Another innovation is the inclusion of a short key to common woods, intended primarily as an exercise in recognizing anatomical features. Many of the illustrations, which are all incorporated in the text for convenient reference, are of different subjects than those used in the other book or found in commercial slides, thus affording students broader experience.

A comment should also be made regarding references. Since it was impractical in a book of this size to mention all of the pertinent literature in the field as was attempted in the larger book, the author has chosen to include essentially only those articles which have appeared since the previous lists were compiled. Needless to say, few botanists have Professor Esau's ability and interest in searching the world literature in this field, so that both the bibliography and text can be expected to be complete and up-to-date. This feature in addition to the glossary should make this book an essential part of every plant anatomist's library as well as an authoritative text for classes in anatomy.

A companion laboratory manual, *Laboratory Guide in Plant Anatomy*, by the same author is also available at a cost of $ 1.75.

DOUGLAS M. POST

TAKHTAJAN, A. L. 1954. "Essays on the Evolutionary Morphology of Plants." Leningrad Univ., Leningrad. Transl. from Russian by Olga Hess Gankin, Ed. G. Ledyard Stebbins. Publ. The American Institute of Biological Sciences, Washington 6, D. C., 1959. Pp. 139. $5·00 (U.S. & Canada), $5·50 (Foreign).

THE scholarly and highly inductive approach followed in these essays makes them suitable only for teachers and advanced students interested in certain fundamental problems of evolutionary morphology. The first essay, devoted to an account of the basic course of development of the science of morphology in the higher plants, is, in the author's own words, not to be regarded "as an original historical study, but as an historical introduction to this book." Essays two to five are concerned with the forms of adaptive evolution, the phenomenon of evolutionary age difference of characteristics, the peculiarities if individual development and the concept of the individual in plants, and with the ontogenetic bases of evolution. The next two essays deal with the role of ontogenetic and teratological data in interpreting phylogenies. The eighth essay is a cautionary note suggesting the limitations of the ontogenetic method, and finally, the last essay is devoted to pointing out some of the basic trends of adaptive evolution of the angiosperms.

In this book, Prof. Takhtajan does not concern himself with the actual mechanism of evolution; he, however, takes up the Neo-Darwinian position and adheres firmly to the principle of natural selection. Prof. Takhtajan distinguishes between three main forms of adaptive evolution: progressive, specialized or particular, and regressive. "While general progress of organization has, so to speak, a universal nature and consists of alterations of a very general character, which are retained in their most basic traits for a long time and even in the course of the subsequent progressive evolution, the particular adaptations are, on the contrary, unstable in the subsequent evolution" (p. 36). "A general regression (general degeneration) of the organism represents the exact opposite of a general progress . . . , in the case of degeneration there takes place a structural and a functional simplification of the organism" (p. 40).

"The periods of general progress are so to speak major evolutionary stages" (p. 37), and involve profound structural and functional modifications, as for example, adaptations connected with terrestrial environment generally. Side by side and especially after each period of progressive evolution there is a period of particular adaptations in which "the systematic ancestral group breaks up into specialized filial groups, which occupy different 'niches of life'" (p. 37). This is adaptive radiation and, according to the author, is very well seen in Psilophytales, seed ferns and primitive angiosperms. Subsequently, the filial groups, particularly those that are less specialized, may become centres of new radiation.

Prof. Takhtajan explains the phenomenon of evolutionary age difference, a combination of primitive and advanced features in the same organism and in the same phylogenetic series (heterochrony of characters), by suggesting that if two structures are not physiologically correlated the evolution of the two may proceed at different rates and along different lines; moreover, "the degree of age difference depends on the degree of the co-ordinative dependence of characteristics as such, as well as on the evolutionary trend and the level of organization of the plant as a whole" (p. 43). He says further that — "In every phylogenetic branch, phenomena of the evolutionary age difference are pronounced to the highest degree in the most primitive group" (p. 43), and that "subsequently, in the process of evolution of primitive groups, the age difference of characteristics becomes usually equalized" (p. 45). His explanation, however, that this "homochrony" of characters takes place "in consequence of evolution proceeding along the pathway of specialization" (p. 45), seems hardly convincing. He asserts that because of specialization, "the organs and the parts of the plant which are not correlatively interlinked, are co-ordinated on the basis of the organism's adaptation to living conditions" (p. 45).

In the chapter on the ontogenetic bases of evolution, Prof. Takhtajan reiterates the concept that alterations in ontogeny produce greater or lesser deviations from the former course depending on whether they occur early or late in ontogeny. Alterations in late ontogeny "produce the least significant deviations" (p. 50). They are expressed in form of excess or defect, e.g. increase and decrease in the size of organs, assymmetry and lobing of leaves, zygomorphy, etc.; also, evolution in these cases shows a continuous pattern. Early deviations in ontogeny, on the other hand, involve changes in primordial stages and result in "sharp, discontinuous alterations" (p. 53) of the organ and organisms. The evolution of monocotyledonous embryo, tricolpate and multicolpate micro-spores, etc., is explained by Prof. Takhtajan in this manner.

"In many instances, the crowding out of the final phases by initial and intermediate phases gradually leads, as it were, to a premature consummation of ontogeny when a more primitive preceding stage becomes transformed into the definitive or adult stage" (p. 55). This is "neoteny" — "protraction of youth". "New significant evolutionary formations may arise when either a premature consummation of ontogeny is subsequently followed by a continuation of the ontogenetic development in a different direction, or the organism deviates from the start more or less sharply from its previous ontogenetic course" (p. 55). "Fixation of the 'embryonic' or another early phase of development usually signifies for the higher plant fixation of its lower tiers and dropping from ontogeny of all 'stories' arising thereafter. A typical plant neoteny is, therefore, a 'tier neoteny'" (p. 55). The reviewers assume that the terms "tiers" and "stories" have reference to the concept of "phasic" and "stadial" development of higher plants.

According to Prof. Takhtajan, neoteny has played a very important role in the evolution of plant forms and he lists numerous examples from "Bryopsida", "Lycopsida", and "Pteropsida", especially Angiospermae. "Many species and genera, as well as larger groups of angiospermous plants have originated by way of neoteny" (p. 59). The duckweeds (Lemnaceae) have "originated not from the adult *Pistia*, but from its embryo" (p. 63). The female gametophyte of *Gnetum*, *Welwitschia* and the angiosperms "originated through a neotenous inhibition of development" at the "initial free nuclear stage of the gametophyte of their ancestors — the primitive gymnosperms, with the subsequent formation of cellular structures entirely new in quality" (p. 63). "The flower originated from the strobilus of the ancestors of the angiosperms in consequence of their neotenous transformation" (p. 125). "Data on the evolutionary morphology of gymnosperms and angiosperms induce me to conclude that the angiosperms are of a neotenous origin" (footnote, p. 124). Also, "herbs have originated from trees by neoteny" (p. 117).

Prof. Takhtajan further points out that, since "evolutionary alterations can occur at any stage of ontogeny", such neotenous transformations provide the organism with "the means of extricating itself" from the "impasse of specialization" (p. 64). They also help to explain, in part, "the absence of transitional forms between many large groups" of plants (p. 66).

Whereas, the basic idea of the author that deviations in early or late ontogeny produce greater or lesser evolutionary changes is sound and is generally accepted, it is rather hard to believe that "neotenous transformations," of the magnitude visualized by the author survived to play any role in evolution. That Prof. Takhtajan does not concern himself with the actual mechanism of evolution makes it easy for him to generalize, but it puts the reader under a strain to understand the validity of the author's conception of neoteny. It appears to the reviewers that the author has confused two ideas voiced by certain authors concerning evolutionary theory: first, the concept of neoteny, and second, the concept that evolution of *major taxa* occurs in one single step, perhaps through the hypothetical "systemic mutations" of Goldschmidt or "typostrophic" mutations of Schindewolf. The gradual dropping out of a later stage and the fixation of an earlier stage in the ontogeny of an ancestor as the definitive and adult stage

of the descendant (neoteny) are conceivable and may have occurred, for example, in the leaf series of *Marsilea*, *Regnellidium*, and *Pilularia* (p. 58); it is unlikely, however, that *major taxa* evolve by means of sudden, sharp, and discontinuous alterations in the early ontogeny. The concept of " saltation " is known to be inconsistent with the facts of genetics and evolution (cf. Stebbins, 1950; Simpson, 1953). Since Prof. Takhtajan has failed to make this distinction, many examples cited by him as evidence of " neotenous transformations " lose their validity.

In chapters 6 and 7, Prof. Takhtajan revives the idea that ontogenetic and teratological data can be used to interpret phylogeny. Although he rejects Hackel's conception of ontogeny recapitulating phylogeny, he insists that because of some " morphogenetic and ecologophysiological" causes some " definite evolutionary stages of distinct characters " are reflected in ontogeny. Because of the peculiar character of ontogeny in plants, these " recapitulations may appear during the successive stages of development of one and the same structure (stadial recapitulations), or they may appear in the early members of a particular series (serial recapitulations). The latter are true " retentions " of paleomorphous characteristics and are evident, for example, in the early members of a leaf series, in a " more primitive structure of the stele at the base of the stem", etc. Numerous other examples of the two kinds of recapitulations are given. Professor Takhtajan, however, is careful in pointing out that " . . . . owing to dropping out of complete stages, swallowing of one stage by another, modifications of stages and heterochrony in the development of characteristics, we never observe in ontogeny a sufficiently perfect reproduction of an organism or of any of its organs and parts, not even in their basic evolutionary stages . . . " (p. 73).

The author admits that most of the teratological cases are mere freaks without any evolutionary significance; however, there are others that cannot be dismissed so easily and which signify an actual " return " (atavism) to the ancestral condition. But, " in atavisms the ancestral structure is never fully reproduced; only individual, more or less modified characteristics are revealed." " In the evolutionary sense there is never any true return to the initial ancestral form. Any atavistic characteristic, appearing in anomalies, is correlatively linked with all modern characteristics of the organism and manifests itself in close association with them " (p. 100).

In reviving these concepts, Prof. Takhtajan, indeed, has rejected much of what was obviously false. However, inspite of his sophisticated and often times involved argumentation and presentation of numerous examples there is, as yet, no proof that these are actual cases of recapitulations and atavisms. Such cases may be reflecting only patterns of development in response to specific environmental factors operating during the ontogeny of a plant. The use of the inductive method is questionable if it derives a theorem from observation of certain facts and then uses the same set of facts to demonstrate the validity of that theorem.

In the eighth chapter Prof. Takhtajan emphasizes that — " A simultaneous and parallel use of the comparative morphological method in its broad sense is the only reliable guarantee that the ontogenetic method will be correctly applied " (p. 116), and in the last chapter he lists his ideas about the basic trends of adaptive evolution of the angiosperms, i.e. evolution of herbaceous habit, conducting system, leaf, flower, and the seeds.

By way of general critism, it should be pointed out that (1) certain statements made by the author need clarification, (2) many examples that are cited do not prove the point in question, and (3) still others are based on erroneous information. Thus, it is said that sometimes " evolution proceeds only by way of particular adaptations " (p. 37), and the presence of primitive traits in *Psilotum*, *Tmesipteris*, *Lycopodium*, eusporangiate ferns, and the Cycadales is cited as an example. The author does not explain what these particular adaptations are.

The apparent resemblance between the early stages of development of sporophyte of Anthocerotales, especially *Notothylas javanicus* and the sporangia of *Horneo-*

phyton (Fig. 11, p. 75) is said to indicate " a well pronounced recapitulation ". It may be appropriate to mention that the derivation of the bryophytes from Psilophytales as a reduction series is still a matter of conjecture; also, it is inadvisable to use one hypothesis to support another hypothesis. Then again, the anomalous cases of " axillary proliferation in coniferous cones " are used as " indisputable examples of atavistic freaks " (p. 107). It should be indicated that, whereas, the occurrence of short shoots with two leaves in place of ovuliferous scales shows that the two structures pertain to the same morphological category, it can not be used as an example of " atavism ", because Florin's work, which Prof. Takhtajan refers to, does not show that at any stage of its evolution the ovuliferous scale was actually a dwarf shoot bearing two vegetative leaves.

On p. 52, Prof. Takhtajan develops Mrs Arber's idea that monocotyledonous leaf should be regarded as a modified fixation of the leaf (phyllome) in its " prelaminar " stage and derives the leaves of monocotyledons from " the prelaminar stage of the primitive leaf of ancient dicotyledons." " The leaves in the Alismaceae and many other primitive monocotyledons are still more or less differentiated into a petiole and a blade. However, in the course of an increasing simplification of the leaf, its adult form approximates more and more the fixed ' prelaminar ' stage. . . . ". It should be pointed out that the situation is not really so simple and that in Alismaceae it is precisely the first formed leaves that are filiform or linear and only the latter ones are differentiated into a lamina and a petiole. Further examples of erroneous statements may be cited: " In the primitive gymnosperms (seed ferns, the Bennettitales and the Cycadales) . . . . . , the rays are heterogeneous, i.e. are composed of morphologically diverse cells — upright (extended along the length of the stem) and procumbent (extended along the radius of the stem) " (p. 121); " Wood parenchyma originated in the secondary xylem of the gymnosperms during the Jura and not earlier, and its appearance was connected with the origin of annual rings " (p. 122). It may be recalled that the so-called " primitive gymnosperms " have rays composed of one cell type only, and that weakly defined growth rings are known in *Callixylon* (Devonian), *Pitys* (lower Carboniferous), and in late Permian forms of *Cordaites*, although none of these forms show wood parenchyma.

Although the essays presented in this book are thought provoking and the basic ideas about forms of adaptive evolution and " modes of deviation " are pertinent and have been well presented, the merit of the book has been undermined by the erroneous citations of examples and by an apparent effort on the part of the author to suit the example to an already formulated system. Only facts suitable to the thesis have been presented and others that might go against it have been virtually disregarded. The result is a text of dogmatic assertions and hardly an objective examination of facts.

The chief merit of the book lies in the first chapter which reflects the scholarship of Prof. Takhtajan in presenting a lucid and very coherent historical account of the pioneering research works in the morphology of higher plants. The book is also rich in citations to Russian literature in botany, many of which, so far, have been unknown to workers outside the Soviet Union. It is understood from the editor of the English translation that the references to works done outside the Soviet Union have been omitted from the bibliography (though not from the text) of the translation.

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